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THE CURVATURE OF ROOTS.

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(WITH PLATE XXVIII)

I. INTRODUCTORY.

In nearly all of the researches hitherto prosecuted upon "curvature" it has been assumed that movements of stems, petioles, leaves, petals, sepals and roots are accomplished by means of similar mechanisms, and the relation of the mechanical elements as well as the phylogenetic meaning of the movement have been ignored. Many writers have gone so far as to uphold the necessity of a common explanation for the mechanism of curvatures of unicellular, coenocytic, and multicellular organs, a necessity by no means obvious. It has been customary also to regard the curvatures of tendrils and other organs highly specialized in structure as well as in function as identical in mechanism with stems from which they are morphologically derived.

In the course of my recently published paper I have shown that great discrepancies exist between the features of curvature of the tendrils of Passiflora and those of stems so far as known. It is quite generally conceded that the curvature of stems is due to the elongation of the side of the member becoming convex, and that the tissues of the concave side are passive or nearly so. It has been shown, on the other hand, that in certain tendrils the formation of reaction curvatures is brought about by the contractile action of a mass of motor tissue lying in the con-

cave side of these organs, and that the elements of the tissue are arranged with comparatively large intercellular spaces in a manner which allows of great and sudden variation in the water contained in the active cells. The action of such tendrils is therefore generally similar to that of pulvini. I have pointed out, moreover, that the features of curvature of the tendrils examined do not agree with those of the stems, and that all tendrils do not produce curvatures in the same manner. Attention has been called to the fact that pulvinar mechanisms may be held to be characteristic of organs in which rapid movement of great amplitude is desirable, and that slower and more general movements, where great tension is essential, are brought about by elongation of the convex sides of the motor organs (14).

In the course of the work upon tendrils, it was found necessary to make some comparisons of the action of certain dorsiventral members of this class with that of young roots of radial structure in the formation of reaction curvatures. The facts concerning the behavior of roots were not described or referred to, and during 1895 and 1896 work upon these organs has been carried steadily forward.

In a general comparison of the conditions prevalent in curving roots and tendrils it is to be seen that while certain general mechanical similarities are present, yet the actual conditions are widely different. The fibro-vascular tissue is in the form of a central cylinder (more or less incomplete) in the tendril, while in the root it is either in the form of a rod or cylinder, but is not fully formed in the motor zone of the root, while tendrils do not acquire the power of reaction until the central cylinder is well differentiated. Furthermore, tendrils are furnished with a subepidermal layer of collenchyma tissue, sometimes two or three cells in thickness; a mechanical equivalent is wholly lacking from most roots. The greatest interest centers in the cortex and its relations to the water conducting or receiving spaces and vessels, since the force which gives rise directly to curvature arises or is released in the cortical parenchyma. In Passiflora the cortex of the tendril is supplied with a great abundance of intercellu-

lar spaces, which may receive any amount of water liable to be freed from the highly permeable motile cells. In other tendrils, in which intercellular spaces are not to be found in the cortex, the connection with the conducting tissue is direct and evident. I have recently called attention to the readiness with which large drops of water exude from the cut surfaces of active tendrils, which indicates the facility with which great quantities may be conducted to or from any point in the organ.[1]

In the motor zone of roots, however, no such intercellular spaces are to be found, and vascular tissues are not fully formed as yet; hence sudden or great variations in the water content of any of the cells in cross section is not possible. As necessary concomitants of these conditions, the movements brought about in roots follow the stimulus only after a much longer latent period, since movement can only be accomplished by alterations in the mass of the entire tissue together, while in tendrils the individual cells are capable of undergoing changes in form and size by giving off or taking up water from the intercellular spaces bounded by their outer walls.

II. HISTORICAL AND GENERAL.

The curvatures of roots have been regarded as identical with the movements of other organs, and the development of the present knowledge of the subject is to be found in the older literature under the title of curvatures. It will be conducive to clearness to recall the more important theses which have received support at various times, so far as the causes of curvatures are concerned. In the special paragraphs dealing with the curvatures of roots, the history of the researches bearing upon the action of these organs will be given.

Perhaps the first actual observation of facts concerned in the mechanism of curvatures was made by Hofmeister (9, p. 88). He found that the extensibility of the epidermal membranes of the convex side of an onion stalk was increased after geotropic

[1] On traumatropic curvatures of tendrils: A paper read before the Indiana Academy of Science, Indianapolis, Indiana, December 1896.

stimulation, and this he believed to explain the curvature. However, he did not regard it as a phenomenon of growth in the present usage of the term, as is to be seen by the following quotation and the context:

> Die auf Einwirkung der Schwerkraft eintretende aufwärts Krümmungen horizontaler oder gegen den Horizont geneigter Organe von Pflanzen geschicht dadurch, dass in der unteren Längshälfte des Organs die Dehnbarkeit diejenigen Zellmembranen zunimmt, welche der Expansion der in Ausdehungsstreben begriffenen Membranen Widerstand leisten.

As a matter of fact Hofmeister believed that the extension of the convex side of a curving root was similar to that shown by a pencil of soft wax.

Sachs, as a result of researches upon shoots and roots, brought out in his *Handbuch* in 1865 (26, pp. 92–96), and again in 1872 (23) and 1873 (24), agrees in the main with Hofmeister, but insists that the exaggerated extension of the convex side of curving organs is an actual growth. This idea was applied by workers in the Würzburg Institute to all curvatures. The development of information concerning turgidity led to an exaggerated estimate of the actual part played by its variations in curvatures.

Since that time, increased turgidity of the cells of the convex side, decreased extensibility of the membranes of the concave side, the aggregation of protoplasm on the concave side producing a shortening of the longitudinal and a lengthening of the radial axes, have each in turn been considered as the motive forces by investigators engaged with the subject. The thorough account of the matter given by F. Darwin in his presidential address to the section of biology of the British Association for the Advancement of Science in 1891 (6) renders it unnecessary to give the detailed steps here

It seems to be agreed on all hands that the curvatures are due to the exaggerated extension of the cells of the convex side, which is accompanied by a diminished extension or contraction of the concave side, dependent upon mechanical conditions. The chief contention at present concerns the conditions attendant upon the extension of the membranes of the convex side.

It may be due to the actual increase in the surface of the membranes, following and caused by the intussusception of new material, and the elongation of the convex side may be an actual growth, as maintained by Pfeffer (18) and others, and which, so far as growth was understood in 1865, is identical with the original explanation proposed by Sachs. On the other hand, the curvature may be due to an elastic and plastic extensibility of these membranes brought about by the induced action of the ectoplasm. Hofmeister's (9) theory of curvature agrees with this in the main, though purely mechanical causes were given for the increased extension of the membranes of the convex side. Sachs admitted the probability of changes in the elasticity of membranes, but he nowhere makes use of the idea in his researches upon the subject. Wiesner held the view that increased ductility of the membranes of the convex side, together with an increased osmotic coefficient, were the causes of curvature (30).

Strasburger also upheld the view that "growth" curvatures are due to increased ductility of the membranes of the convex side, and called attention to instances of changes of ductility in the walls of Oedogonium, the branching of Cladophora, and similar occurrences (29). Noll has recently brought some striking experimental results which, in connection with his previous work, go far to establish variations in plastic and elastic extensibility of the membranes as primary factors in the mechanism of curvature (16).

III. THE CURVATURES OF ROOTS.

I have indicated above that the constantly increasing mass of facts shows many differences between the phenomena attendant upon curvatures of roots and shoots, and it will be necessary therefore to recall the principal researches directed toward the mechanism of curvatures of roots, but it will not be profitable to go back of the work of Hofmeister. In the earlier researches, to which reference has been made above, Hofmeister sought to establish that in apogeotropic organs, such as roots, longitudinal

tensions do not exist, and that downward curvature is purely mechanical, in confirmation of the theory originally proposed by Knight in 1806 (9). Frank, a few years later, demonstrated conclusively that the apogeotropic curvatures of roots are not mechanical, or due to the plasticity of the root tip and its own weight, but are due to active physiological processes (7). Despite the facts presented by Frank, Hofmeister maintained in a later paper:

> Alles ist so concludent wie möglich und lässt nur den Schlus zu, dass bei der Abwärtssenkung der äussersten Ende wachsender Wurzeln eine nahe hinter der Spitze gelegener Querabschnitt der Wurzel in ähnlicher Weise passiv dem Zuge der Schwere folge, wie ein zäber Brei oder ein Tropfen steifen Lacks (10).

Frank, however, firmly established the active part taken by the root in producing curvatures, and all later researches upon the subject are based upon this fact, and attention has been directed to the localization of the sensory and motor tissues, and the determination of the individual factors active in curvature.

Cieselski made an examination of the mechanism of the curvature of roots in 1871, in connection with his remarkable researches upon the general nature of irritability of these organs (1). He noted for the first time the greater density of the protoplasm of the concave side of the organs, a fact confirmed by Kohl in unicellular or coenocytic plants, and later in stems and tendrils by Sachs, and further examined by myself. The greater density of the protoplasm in the concave side of a tendril is not conditioned upon curvature, however, but is a distinct morphological character apparent in the earlier stages of development, before the special forms of irritability characteristic of these organs are exercised or even manifested. This aggregation of the protoplasm upon the concave side of isodiametric unicellular and multicellular organs has been described by Wortmann as the primary factor in the cause of curvature, an explanation which has been found inadequate for reasons which need not be discussed here. During a period from 1871 to 1873, Sachs devoted a large share of his attention to the curvatures of roots, and, so

far as the mechanism of curvature is concerned, he concludes that it is due to the exaggerated growth of the convex side. Later researches by various investigators were turned toward other special phases of the subject and will be treated under the proper heads.

It has followed, as a result of the various investigations named above, that the immediate cause of curvature of roots and similar parts must be looked for in the cell wall, rather than in the ectoplasm. In certain tendrils, on the other hand, the immediate cause of the curvature is the alteration in the motility and permeability of the ectoplasm. It is of course true that the changes in the cell wall in roots must be induced by the ectoplasm.

It has appeared to the writer that the more important facts concerning curvature might be obtained by an actual examination of the changes of cell contours and wall characters in the motor zones of the curving organs, in the manner which has yielded such decided results in the study of tendrils, and which has been applied to some extent by Kohl in unicellular organs, and especially by Noll in his study of stems. The result may apply to all isodiametric organs, but the writer does not wish to make such strict and inclusive application, since it is conceivable that the disposition of the mechanical factors, as well as the development of the various forms of irritability, would necessitate in many cases a somewhat different method of procedure.

IV. DEVELOPMENT OF IRRITABILITY IN ROOTS AND SHOOTS.[2]

The emergence of the plant from an aquatic to a terrestrial habitat, in connection with the loss of motility in an extremely early stage of its development, was marked by several radical changes in its physiological organization, due in greater part to the alterations in the conditions attendant upon the nutritive processes.

The economical acquisition of nutritive substance in proper

[2] Given in an address before the Botanical Club of The University of Chicago, January 18, 1897.

amount is a fundamental necessity of every organism, and to the conditions attendant upon the performance of the nutritive functions must be ascribed the chief causes underlying the development of the plant body. The chlorophyll processes, therefore, have been the paramount factors in the development of the shoot, and the necessities attendant upon their proper performance will account for the method of differentiation of the shoot, and the very great degree of segmentation and branching which it has attained. The segmentation of the shoot has made possible not only the profitable display of ever increasing areas of chlorophyll bearing tissues, the proper elevation, orientation, and isolation of the reproductive organs, but also a separation of the minor functions and the differentiation of special organs for their performance. The separation of nutritive, reproductive, and other functions has been accompanied by a contemporaneous separation and development of the special forms of irritability which are concerned with the forces dealt with by each organ. Thus, for example, the most important factor in the processes carried on by the leaf is the radiant energy derived from the sun. As a necessary concomitant of the advantageous use of this energy, the leaf has developed a strongly marked irritability to light and heat rays, and, as a result of the relations of the organ to the horizon in response to its heliotropism and thermotropism, it has acquired in some instances also a trace of geotropism.

In the accomplishment of the reproductive processes, an incidental condition is the transference of the pollen from its place of formation to the surface of the stigma in the same or other flowers. In a great majority of instances the relation of the line joining the anther and the stigma to the vertex or horizon is of the utmost importance, whether the pollination is accomplished by insects or automatically by air currents, and a well marked geotropic reaction is therefore generally exhibited by flowers with the motor zone located in the peduncle. These organs also show minor heliotropic reactions.

The same process of analysis may be applied to the entire

shoot, with the general result that each organ will be found to respond to a number of forces generally limited to two or three, though, of course, instances are not lacking where a great number of forms of irritability are found to reside in the same organ, as, for example, in tendrils. In such instances, however, the excessive number of the forms of irritability has been developed to meet special ecological conditions, bearing upon both the nutritive and reproductive processes, either directly or indirectly. Furthermore, the organs of the shoot may acquire also the power of special reactions to internal forces or stimuli, such, for example, as the carpotropic movements.

In a consideration of the localization and distribution of the property of irritability attention is to be called to the fact that the conditions concerned in the nutritive processes of the shoot show an invariably wide diffusion in space, while varying from zero to maximum in time. Carbon dioxide exists everywhere in the atmosphere in uniform proportions and bathes every part of the shoot. Sunlight is bounded only by the horizon line, and may reach any surface of the shoot in diffuse form. The chlorophyll processes may then be carried on by the subepidermal tissues in any portion of the shoot, and as a consequence a greater proportion of the peripheral protoplasm of the shoot has developed an irritability to sunlight, although it may not always be manifested by organic or external movement, or other response.

The researches of Rothert have shown that a large part of the surface of the leaf of Avena and Phalaris exhibits a heliotropic irritability, and some experiments in my own laboratory, by Mr. R. E. Squires, demonstrate that the laminae of dicotyledonous leaves exhibit an equal distribution of sensitiveness over their entire surface, and that the leaflets in a compound organ are strictly coordinate and equal with respect to their irritability (22). Those branches of the shoot that have developed special or ecological adaptations exhibit an extension of the irritable surface corresponding to the limited diffusion or

occurrence of possible stimuli, modified to some extent by the character and inclusiveness of the reaction.

Although the motor zones of the shoots do not include as large proportions of the plant as the sensory zone, yet the distribution is fairly general throughout the growing regions. It is possible to induce curvatures in some stems in which growth has almost entirely ceased. The curvature, however, is accompanied by a revival of the growth activity.

The functions of the root are not so numerous as those of the shoot, and while the efficient performance of the necessary amount of absorption to keep pace with the increase in mass and surface of the shoot has demanded a repeated branching, yet no segmentation like that of the shoot has occurred. The secondary function of the root, fixation, is purely mechanical, and the separation of the two functions has not been effected by a localization of the functions in different organs, but is an incident to the stage or degree of development of these organs. Physiologically the basal portion of roots sustains a relation to the absorptive system similar to that of the basal portions of typical stems to the chlorophyll bearing and reproductive organs.

In the earlier stages of growth any given portion of the root is purely directive, next absorptive, and in later periods is exclusively fixative. Only in certain special classes of aerial and other plants does a separation or isolation occur. The stem, on the other hand, is at first directive, and then fixative, and does not in any stage of its existence assume the relative importance which is to be ascribed to every portion of the root in one period of its development.

In explanation of this different method of development it is to be said that the roots have always been surrounded by much more uniform conditions in time than the shoot, and in consequence have met the necessity for a much narrower range of adaptive modifications. But while the range and rapidity of variation of outward conditions affecting the roots have been much less than those of the shoot, yet the inequalities of diffusion and distribution of the nutritive factors are much greater than those

affecting the shoot. Water and food substances lie below the surface of the substratum, and the root has developed a highly marked form of geotropism, which enables it to penetrate the soil. Water and food substances, however, are by no means so uniformly distributed as sunlight and carbon dioxide. While water exhibits a fairly horizontal distribution in quantity, yet so far as its actual availability is concerned differences corresponding to the physical characteristics of the soil are to be found. The vertical distribution is modified in the same manner. The mineral food substances present no system or uniformity of distribution whatever. As a matter of fact the masses of food substances may and do lie in all possible directions from the absorbent zone of the apical portion of the root. In order to reach such irregularly distributed masses of nutritive substances it is evidently necessary that the root should develop an irritability to a much greater number of forces than any member or organ of the shoot, and furthermore it is evident that all the forms of irritability thus acquired must be located in the apical portion of the root, the proper directive activity of which only is concerned with the absorptive processes. The coincidence of several forms of irritability within such narrow limits has necessitated differentiations in another direction from that offered by the shoot. The differentiation of the shoot resulted in a tendency to separate the different forms of irritability with their attendant mechanisms. The increase of the efficiency of the root has resulted in the acquisition of a constantly increasing number of forms of irritability, within a limited mass of tissue, the mechanism of which must necessarily be identical. Still further this has resulted, of course, in the differentiation of the separate parts of the mechanism and increase of its delicacy of reaction. This may be held to apply to all similar arrangements, especially in the ecological reactions shown by the so-called "sensitive" plants.

V. IRRITABLE ORGANIZATION OF THE ROOT.

On account of the fact that the irritable mechanism of roots is located in the embryonic region of the organ, no distinct

morphological characters can be assigned to the various organs of irritability. As a matter of fact the differentiation is entirely physiological, as it will be, indeed, in all organs in which the irritability is only a temporary character. It is therefore impossible to do more than to determine the relative position of the masses of cells in which in turn the various parts of this complex function are located.

VI. FORCES ACTING AS STIMULI IN ROOTS.

In accordance with the above it is found that the roots react to geotropic, heliotropic, thermotropic, hydrotropic, galvanotropic, rheotropic, chemotropic, and traumatropic stimuli, besides exhibiting rectipetality or autotropism. These terms are used in an inclusive sense, without reference to the phase of reaction under each form. Under traumatropism are included all of the reactions to mechanical stimuli, resulting in contact or injury, as well as the action of corrosive chemicals. It is to be noted that many roots do not exhibit all of the forms of irritability enumerated.

In the study of the mechanism of curvatures which forms a part of this paper I have examined geotropic, rheotropic, and traumatropic curvatures, and since no essential difference could be detected, chief attention was paid to curvatures obtained by geotropism.

VII. THE SENSORY ZONE.

The history of the researches bearing upon the location of the sensitive tissue of the root is a long one, and begins with Darwin's experiments in which decapitated roots were found to be incapable of response to the forces to which they usually react (4). The pathological condition induced by the decapitation made the conclusion that the sensitive tissue was located in the extreme apex unsafe, and it was bitterly opposed by Sachs (28), Detlefsen, and others, and it was not entirely determined beyond doubt until the recent brilliant experiments of Pfeffer (21), in which it was shown that if a root were forced to grow in a bent

tube in such a manner that the section 1 to 2^{mm} in length, including the *punctum vegetationis*, assumed a position at right angles to the axis of the basal portion, and then placed in such position that the bent apex was in a position of equilibrium, no excitation occurred. A concise history of the various researches dealing with the localization of the sensitive tissue, previous to the experiments of Pfeffer, was given by Rothert in 1894 (21).

The result of all the investigations upon the matter shows that the mass of sensitive tissue is located in the peripheral portion of the *punctum vegetationis*. The excision of a mass of cells not exceeding $.5^{cu\ mm}$ removes this zone of sensitive tissue entirely from the roots of *Zea mais*, and since the penetration of the growing zone beyond the outer layers produces other effects besides those due to irritability, it may be assumed that the sensitive tissue is in the form of a cup with walls consisting of a few layers of cells only. Furthermore, the cells of the walls of the cup acquire the special power of reception of outward stimuli shortly after their formation, and retain it for a short time only, during which time the *punctum vegetationis* moves forward and forms new layers in front of them. This period in most roots extends over a few hours only. After this time, these cells lose the power of converting impinging forces into impulses, and retain only the primitive forms common to all. Whether or not this specialized mass of cells, or rather the cells in the specialized stage, are arranged as a complex organ, in which the individual and separate action of the cells is necessary, or whether each individual cell is capable of giving rise to the force constituting an impulse, has not been ascertained, since insurmountable technical difficulties stand in the way of a determination of the matter. It appears more likely, however, that the concerted and organized action of a number of the protoplasts of the irritable zone is indispensable, especially in such reactions as those of geotropism.

This conclusion is favored by results obtained by Spalding in his study of traumatropic curvatures (28). He says:

It soon became evident that the nature, direction, and extent of the wound

constitute an important factor. . . . . If the tip of a root is cut off square across, it does not exhibit traumatropic curvatures, but if cut obliquely it becomes curved, provided the cut is made to the right depth. . . . . It is plain that in order to induce traumatropic curvature with certainty by oblique cutting away of tissue at the apex, the cut must be made deep enough to affect the growing point itself. It is perfectly plain that the root cap may be cut deeply without curvature following.

In my own work some experiments were made in an effort to bound the sensory zone. A root tip of Zea, branded in such manner that nearly all of the root cap was killed, as well as a sector of tissue beginning .5^{mm} back of the apex of the growing point and extending obliquely across, intersecting both sides of the cylinder of periblem and including the entire apical part of the growing point (*fig. 1*), exhibited marked curvature a few hours later.

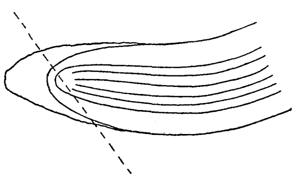


FIG. 1

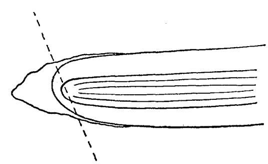


FIG. 2

FIG. 1. Diagram showing extent of injury by branding, producing a curvature in a root of Zea.

FIG. 2. Diagram showing extent of injury by branding, producing a curvature in a root of Pisum.

In another instance, a root of Pisum, branded in such manner that the entire root tip and a sector .4^{mm} in length (axially) cutting both sides of the cylinder of periblem at an angle of 30°, produced a curvature (*fig. 2*). A strong curvature was exhibited by a root of Phoenix from which a thin slice from the outer layer of the cortex back of the *punctum vegetationis* had been removed (*fig. 3*). In like manner, a radial incision in the cortex of a root of Arisaema at a distance of 1.5^{cm} from the tip gave a decided reaction (*fig. 4*). These results suggest that the sensitive zone includes that portion of the periblem lying basal to the perpendicular through the axis of the root at the growing

point, and that this tissue is in the form of a cone shaped cup, the rounded bottom of which is extremely thin, or is wholly absent.

As a matter of fact, it appears from the results at hand that the *punctum vegetationis* does not form a part of the sensory zone. Some further investigations upon this point are in progress. It is highly improbable that the growing point, shielded by the thick root cap, should have acquired any special irritability to

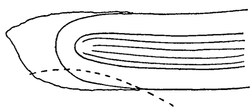


FIG. 3

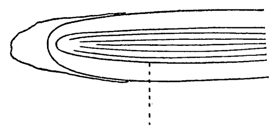


FIG. 4

FIG. 3. Diagram showing extent of excision producing curvature in a root of Phoenix dactylifera.

FIG. 4. Diagram showing location and extent of incision producing curvature in a root of Arisaema triphyllum.

external forces, particularly of a mechanical nature. It is to be remembered that the specialized receptive zone of the root tip is a physiological, not a morphological differentiation. This zone resides in the embryonic tissue during a limited number of hours only, and moves steadily forward. Furthermore, this single zone is capable of the reception of stimuli of all the classes to which the root as a whole reacts, eight in number. It is to be noted that in irritable mechanisms of such character the phenomena of accommodation may not occur. The residence of the special forms of irritability is too brief to permit the protoplasm to recover from continued stimuli. In the root the period of irritability is but little greater than the latent period.

This region, capable of receiving special stimuli and originating motor impulses, has been termed the *perceptive zone*. I am unable to trace such an application of the term to its origin, but find that it has been in use in the publications of the botanical

institute at Leipzig since 1893 (18). Such a usage of the term is not in harmony with the meaning of "perception" in the domain of psychology, since here it is used to denote a much higher form of activity, coupled with the presence of consciousness, or a much higher form of consciousness than is exhibited by roots, and the use of the word "perception" to denote any of its functions is therefore wrong and misleading. It is evident that the most appropriate term must be derived from the term *sensor*. The following use of the term by Clifford (3, **2**: 108) will illustrate quite fully the significance of the term:

> Various combinations of disturbances in the sensor tract lead to the appropriate combination of disturbances in the motor tract.

I have therefore denoted this specially irritable zone as the *sensory zone*. Some sharp distinctions exist between the general nature of the sensory zone of roots and that of tendrils and other special forms of irritable organs, in which a similar coincidence of several forms of irritability occurs. In the latter, the sensory zone is composed of morphologically differentiated protoplasts which retain their directive function during the entire period of activity of the organ of which they form a part, and although they give rise to impulses in response to several classes of stimuli, the reaction, with minor modifications, is invariable in kind and direction, and shows differences in degree due to the specialization of the motor tracts, which retain their function during the activity of the member of which they are a part. In roots, on the other hand, the sensory function moves steadily from protoplast to protoplast, as also does the motor function; and while the sensory zone converts many different classes of stimuli into motor impulses, yet the reaction is by no means invariably the same. The root may move toward or away from the different stimuli, or may move toward an amount of stimulus, constituting its optimum, and move away from a greater intensity of force. The greater inclusiveness of the purpose of the root is of course accountable for the wider range of reaction; and it is also to be said that it is a natural result of morphological necessity and physiological economy.

VIII. THE LATENT PERIOD.

The latent period embraces the time necessary for the conversion of the external force into an impulse, the transmission of the impulse to the motor zone, and the changes in the motor zone necessary to exert a bending force upon the root.

Although no special and exact measurements of the latent period were made in my experiments, yet it was found in plants, such as Pisum and Phaseolus, in which a primary medulla is formed and the mechanical tissues of the motor zone are thus in the form of a tube, the latent period was from three to five hours. On the other hand, in such roots as those of Zea and other monocotyledonous plants, in which the fibro-vascular tissue is in the form of a solid cylinder of less diameter than the tube in Phaseolus, it would present far less resistance to the action of the cortex. The latent period of Zea is from one to two hours. It is to be borne in mind that in all such observations the roots were under conditions which retard curvature. The latent period of roots in the soil must be somewhat less. Chas. Darwin notes distinct curvatures in the roots of many plants, in response to contact, in five to nine hours (4). The movement had made great progress (20–30°) on the lapse of this period after excitation. It is evident that wide variations will be shown in the length of time between excitation and reaction.

The manner in which impulses are conducted from the sensory to the motor zone is a matter which may not be determined exactly. The entire mass of protoplasts between the sensory zone and the motor zone are in a state of intense metabolism and vigorous growth, and are not entirely separated by the imperfect and newly formed walls. The distance separating the two zones may be as great as 1 to 2^{mm} in some roots in a state of very rapid elongation, while in others the two regions must nearly join; indeed, it is conceivable that they may overlap in certain cases (see "motor zone").

The determination of the method of transmission is a matter which must wait upon a great advance in knowledge of the physiology of the cell.

The assumption is justified that the great difference in the latent period is due to the greater mechanical inertia to be overcome in Phaseolus than in Zea, and that only a comparatively small proportion of it is concerned in the production and transmission of the impulse. That many changes preliminary to curvature do ensue is suggested by the results of Kirchner (11), who found that a marked difference was to be noted between the specific gravity of the tissues of the convex and concave sides of a root in one to two hours after stimulation, or long before the slightest curvature was to be seen.

IX. THE MOTOR ZONE.

The region of the root which exhibits curvature is to be termed the *motor zone*. Hofmeister asserted that the region capable of curvature occupies a position immediately back of the root cap, and found by twenty measurements that it lies at a distance of 1.75 to 3^{mm} from the tip of the root cap in roots of Pisum (10). Frank (8), N. J. C. Müller (15), and Cieselski (1), on the other hand, held that the curvature occurs in the region of greatest growth; and Sachs (27), in consideration of these conflicting views, asserts that the entire growing region of the root participates in the action, and that naturally the region of most rapid elongation exhibits the curvature of the shortest radius. The proper determination of this matter is of the greatest importance in the consideration of the mechanism of curvature. If the entire growing region participates in the movement it would be a very weighty bit of evidence in favor of the theory that curvature results purely from growth, to the exclusion of any idea of ductile extension. If, however, only a special region is concerned the case is left open for the interposition of specialized action on the part of the root. This specialized action might consist of accelerated growth or might consist in changes in extensibility of the walls.

An examination of my preparations reveals the fact that the region of greatest curvature lies in that portion of the root where the energy of the periblem or cortex has become diverted

from cell division to cell enlargement, and where the walls exhibit the greatest extensibility. The forward edge of this zone lies at a distance of 2 to 2.4^{mm} from the forward limit of the *punctum vegetationis* in Zea. The measurements were made of sections of roots which had been under geotropic excitation for three hours and were then killed in chromic acid. During this time the region forward of the motor zone had doubtless increased in length at its usual rate, and the measurements thus include an increment of growth amounting to 10 to 15 per cent. of the total length given. This fact has been wholly disregarded in the determinations hitherto made of the location of the motor zone. The distance from the tip to the region of curvature often measures 8 to 20^{mm} twenty-four hours after excitation. The excitation sets certain forces in play in a region at a certain distance from the tip at the time of excitation. The apical region continues to elongate, and by the time the motion becomes visible the apex has extended its own length considerably.

That the curvature does not extend over the entire region of growth according to its condition is to be seen in a comparison of the curvatures obtained mechanically and those resulting from the geotropic reactions. Sachs has urged as objection to the localization of the motor zone the argument that many of the results pointing to this conclusion have been obtained from abnormal conditions, the foremost of which he assumes as the placing of the root in such position that its tip projects above the horizontal. He assumes that the greatest geotropic stimulation is obtained when the tip is horizontal. This has been disproven by recent investigations, which have demonstrated that geotropic excitation increases in force as the tip approaches the vertical pointing upward.

Sachs urged that the curvature obtained by roots placed in such position underwent minor excitation, in accordance with his theory that the entire growing region is geotropically sensitive as well as motile. The recent confirmation of Darwin's theory of the localization of the irritable cells in the apex of the

root renders these objections invalid, since it is the relation of the sensory zone only to the vertical which affects the movement.

If the curvature is distributed according to the rapidity of growth the geotropic curvatures should, according to the theory of Sachs, resemble those obtained by a mechanical curvature of the root, since the normal extensibility of the walls may be assumed to be in direct proportion to the rapidity of elongation. The curves obtained by mechanical bending of roots are not in accordance with those attributed by Sachs to geotropism. The radius of curvature is shortest in the region of most rapid growth and gradually elongates in both directions. In geotropic curvatures, however, the difference between the radii of curvature of the forward portion of the region of rapid growth and the apical and basal portions is abrupt and marked, showing that a special region has effected the greater part of the curvature. In this region the cortical and vascular cells have not attained more than 25 to 35 per cent. of their final length. The minor curvature, which includes the basal and apical portions of the root, may be explained entirely as mechanical results of the disturbance of tensions by the action of the cells of the specialized zone, and, as a matter of fact, are reproduced exactly in mechanical curvatures. At any rate these minor curvatures actually disappear with the fixation of the organ in its new position. In conclusion of this detail, it is to be said that the formation of a sharper break or angle required by Sachs to establish the theory of a localized motor zone is not consequential in a body so plastic as the growing portion of the root.

In connection with the question of localization of curvatures the facts obtained as to the behavior of a root in recurvatures are of value. It has been quite generally asserted and received that if a geotropically excited root were allowed to effect only a small amount of curvature, and then placed in a position which would induce a curvature exactly opposite, the first curve would be obliterated.

I have directed some experiments to this phase of the ques-

tion in the following manner: Seedlings of Zea were placed in such position that the roots were pointing nearly vertically upward for a period of five hours and a curvature of 50° had ensued. At this time the root was reversed and placed in such position that a curvature would be induced in exactly the opposite direction. This curvature was allowed to proceed for fifteen hours, until it was much more marked than in the first instance. The roots were then killed and hardened in chromic acid in the usual manner. The sections thus obtained show that such curvatures cannot be obliterated (see table XII).

While in most roots the motor zone lies forward of the root hairs, sometimes the hairs may attain considerable length before the curvature is entirely accomplished. In Zea the papilla like extensions were to be seen often in the apical part of the motor zone three hours after excitation, and the tubes had attained a length equal to many times their diameter in curvatures eight hours after excitation. That is to say, the zone of root hairs had moved forward until it embraced the region of curvature before motion had entirely ceased. No difference of structure or form could be made out between those of the convex and concave sides. It is to be seen that the movement would often result in the rupture of the hairs on the region of curvature, especially on the convex side.

In this zone the annular vessels are represented by great cells with a length of 0.75 to 1.^{mm}, and a diameter of 0.2 to 0.3^{mm}. The nuclei are still present and a distinct lining layer. The remaining vascular elements are still in the form of elongated cells in which the protoplasmic content and no differentiation of the wall have appeared. The cortical parenchyma is in the form of short cylindrical cells with the ends in some instances slightly rounded and in others distinctly plane.

X. THE MECHANISM OF CURVATURE.

In the examination of the curvatures of roots in order to determine the forces active in producing curvature I have used specimens of *Zea mais*, *Phaseolus vulgaris*, *Pisum sativum*, *Ari-*

saema triphyllum, and *Phoenix dactylifera*. On account of the fact that Zea has been used in so many researches of this character, and because so many of the minor features are well known, I have taken it through every phase of treatment.

It is universally admitted on all hands that the forces actually productive of curvatures are manifested in the newly formed cortex of the convex side of the root, and the point upon which question is raised is whether the elongation of the cortical cells is due to actual growth of cells or is due to a sudden induced ductility and elasticity of the longitudinal membranes. As will be seen below my results give direct evidence upon this point.

The first direct work upon this point was done by Cieselski (1), who concluded that the changes in the motor zones of curving roots consist chiefly in a greatly exaggerated increase in size in all directions of the cells (of the cortex) of the convex side, and not only a decreased growth of the cells of the concave side, but also a compression of these cells. The cells of the convex side are enlarged in all three axes, and the cells of the concave side in every axis are below the average size, while the walls are wrinkled and folded. Since Cieselski's work has been made the basis of so much recent work which must be corrected in the light of my own results, I quote his paragraph containing this matter in full, and reproduce the figure showing the structure of a curved root.

Schon die der Untersuchung des Langschnittes einer solchen stark gekrümmten Wurzel fallt es auf, dass die Zellen der Epidermis und des Rindenparenchyms der unteren concaven Kante vielfach gegeneinander verschoben, keilformig zusammengedruckt sind, und nicht selten Falten in den aüsseren Conturen des concaven Bogens erscheinen, während die obere convexe Kante eine gleichmässige Spannung und stark ausgepragte, regelmässige Entwickelung der entsprechenden Zellen zeigt. Das mikroskopische Bild überzeugt uns hiernach mit voller Bestimmtheit, dass die an der convexen Seite gelegenen Zellen eine abnorme Streckung nach allen Richtungen erlitten und dadurch die Zellen der concaven Kante nicht nur an der entsprechenden Vergrösserung gehindert, sondern sogar comprimirt haben, wie dies die vielfachen wir nun die Grosse der Zellen an den beiden Kanten genauer, so finden wir, dass die der convexen nicht blos der Lange nach, sondern auch nach den beiden anderen Dimensionen weit über das normale Mass ausgedehnt haben,

während die Zellen der concaven Kante zusammengedruckt erscheinen und in ihren drei Achsen bei weitem hinter dem Mittel zurückgeblieben sind. Vergl. *fig. 4*. (*Plate XXVIII, M.*)

Aus vielen Messungen, die ich an stark gekrümmten Wurzeln ausgeführt habe, führe ich nur eine beliebige an; die Werthe sind hier das Mittel aus je 5 Messungen, und zwar betreffen diese nur die erste an der Epidermis gelegene Schicht des Rindenparenchyms der beiden Kanten der Krümmungsstelle und dann einer Region weiter unten, wo die Wurzel gerade senkrecht abwärts sich entwickelt hat; es ist noch zu bemerken dass alle Zellen bereits ihr Wachstum vollendet haben.

Die Grosse der Zellen der erwahnten Schicht betrug:

	Lange	Breite	Dicke
an der convexen Kante, - - -	0.125^{mm}	0.045^{mm}	0.042^{mm}
an der concaven Kante, - - - -	0.020^{mm}	0.025^{mm}	0.026^{mm}
bei normaler Ausbildung - - -	0.099^{mm}	0.035^{mm}	0.032^{mm}

Cieselski's assertions were not fully confirmed by Sachs' work of the following year. Some incomplete observations by Sachs pointed to the conclusion that curvature was accompanied by an accelerated increase of the radial diameter of the cortical cells of the concave side, and a retardation of the radial increase of the cortical cells of the convex side. He says (24, p. 469):

Einige noch zu vervollständigende Beobachtungen (s. oben) weisen darauf hin, dass die Retardation des Längenwachstums auf der Unterseite mit einer Steigerung, die Beschleunigung des Längenwachstums auf der Oberseite mit einer Beeintrachtigung des Wachstums in radialen Richtung verbunden ist; die Zellen der concaven Seite machen auf den Beobachter den Eindruck als ob sie in der Längsrichtung comprimirt, daher in die Querrichtung erweitert, der die convexen Seite dagegen als waren sie in der Längsrichtung gezerrt und dabei verengert; dabei stehen die Querwände der Zellen der concaven Rinde radial, in der convexen Seite sind schief und prosenchymatisch zugespitzt.

This conclusion is based upon the following measurements. Roots of Vicia were allowed to curve for fourteen hours, and then the distance between marks previously placed upon it were taken by readings with the microscope.

VICIA FABA.

Amount of growth in length	
Convex side, - - - - -	5.8^{mm}
Concave side, - - - - -	2.8^{mm}

Median line, - - - - - -	4.3^{mm}
Normal root, - - - - - -	5.5^{mm}
Acceleration of convex side, - -	0.3^{mm}
Retardation of concave side, - - - -	2.7^{mm}
Retardation of middle line, - -	1.2^{mm}

In a number of measurements of the length of the cells of the cortex of the convex and concave sides Sachs found the convex exceeded the concave in these ratios of 1:1.6, 1:1.8, 1:2, and 1:3.4. It was to be said, therefore, that the cortex of the concave side gains in length and breadth at the same time, but at a rate much below the normal. This statement has also been held to apply to all tendrils by Sachs as well as de Vries.

Noll has also paid some attention to the comparative changes in the size and contours of the convex and concave sides of curving shoots (1888) of dicotyledonous and monocotyledonous plants. He has from the beginning of his researches steadily advocated the theory that curvatures were due to an induced increase in the ductility of the membranes of the convex side, and has adduced some very conclusive evidence in his most recent paper on the subject (1895).

In the descriptions of the actual contours of the motile cells in the zone of curvature he confirms Cieselski's view, that the cells of the convex side increase in every diameter so far as stems are concerned. Thus, he says (15, p. 526):

> Wie eine genaue mikroscopische Untersuchung, oft aber auch schon der erste Anblick lehrt, werden die Zellen der Konvexseiten bei der Krümmung nicht nur länger, sondern auch breiter und höher. Wenn auch die Zunahme in der einen Dimensionen doch zuweilen das Doppelte erreichen und übertreffen, wie es besonders bei Grasknoten oft wahrzunehmen ist.

This statement is confirmed by drawings made with a camera lucida, and must therefore be accepted as a fact. However, none of these drawings include sections of roots. A measurement of the drawings shows that in the radial diameter of the epidermal cells of the grass the concave exceeds the convex in the ratio 1.1 to 1, and in the epidermal cells of the Vicia in the ratio 77:66. A similar relation is to be seen in some later reproductions (16, pp. 73, 74) of the radial outlines of the epi-

dermis and collenchyma of the curving region of stems of *Vicia Faba*. Cieselski's results were based upon experiments with Zea, Vicia, and *Ervum lens*, and Sachs' results upon Pisum, Phaseolus, Cucurbita, Quercus, Polygonum, Lepidium, Zea, Triticum, Vicia, and Æsculus. So far as I have examined the above mentioned species my conclusions as to the behavior of the cortical cells of the convex side agree with those obtained by Sachs. But in material, such as the roots of Phoenix, presenting different mechanical conditions I have found an action of the convex side similar to that wrongly ascribed to Zea by Cieselski. I am at a loss to account for his mistake in the matter.

XI. SCOPE OF EXPERIMENTS.

In addition to the experimental results adduced in the preceding portions of this paper, chief attention has been paid to the collection of data bearing upon the mechanism of curvature, with reference to the character of the changes ensuing in the motor zone during curvature. To this end a series of experiments was devised by which reaction curvatures were obtained in the following manner: Geotropic curvatures were obtained by placing seedlings in such position that the radicle pointed nearly vertically upward, and the curved portions, inclusive of the apex, were taken, some at three, others at eight, twenty, and seventy hours after the excitation began. The roots were in moist air, sawdust, or earth, at temperatures between 16 and 20° C. Mechanically curved preparations of the motor zone were made as follows: Two pins were driven in a plate of moist cork at a distance apart slightly in excess of the diameter of the apical portion of the root. The root was thrust between these pins in such manner that when the basal portion was moved to one side a curvature would be produced in the motor zone. To accomplish the bending a third pin, placed against the side of the root, was slowly moved laterally until the root was bent at right angles when the pin was thrust in the cork, and the entire preparation immersed in a hardening solution. Some

illuminating comparisons were obtained from this material. In order to determine, if possible, the nature of the changes induced in the motor zone previous to reaction, seedlings were placed in such position that the radicles pointed nearly vertically upward. After a time, approximately equal to the latent period of the organ, the motor zone was bent mechanically in the plane in which curvature would have ensued if the roots had been allowed to react normally. The bending and killing was accomplished as above.

Traumatropic curvatures were produced for the study of the motor and sensory zones as follows: The tips of roots were touched with acetic acid or a hot rod, or cut with a razor in the manner described by Spalding (28), and then the seedling was placed in a moist chamber or moist sawdust. Roots which were to be placed in the moist chamber could be branded by means of a glass rod heated in the yellow gas flame. The adhering portion of carbon served to mark the location and direction of the branding. It is to be said that in general traumatropic reactions exhibit a much longer latent period than those of geotropism. In some instances branded roots were placed in such position as to be geotropically excited at the time, although no uniform acceleration of curvature was thus obtained.

So far as the information of the writer is concerned, it does not appear that any attempt has been made to obtain the anatomical details and stature of the cells of the motor zone in a root in which the curvature recently produced has been straightened by an excitation in the opposite direction. No exact data are accessible, but almost all of the writers who have dealt with the subject are unanimous in the agreement that young curvatures may be straightened and equalized. The material bearing upon this point was obtained by placing root tips pointing upward until various angles of geotropic curvature had been formed, and then by a half revolution of the basal portion of the root upon its axis and the proper lateral adjustment, the tip was brought into a position similar to the original

with respect to the vertical, but with the excitation tending to induce curvature in the opposite direction. The results obtained from the sections of roots thus treated form by no means the least important part of this paper.

XII. PREPARATION OF SECTIONS.

In the determination of changes in the motor zone it is of the greatest importance to kill and fix the tissues with no disturbance of the existing relations of the membranes, and to cut sections in the plane of curvature through a region embracing the root cap and the region lying between it and the motor zone, and a portion of the root basal to the motor zone. Furthermore, it is highly desirable that the sections made under different conditions should be made permanent and held for comparison. Simple as this matter may seem, it does not appear to have been done by any of my predecessors. The roots were killed, hardened, and fixed in a 1 per cent. solution of chromic acid, in which they were allowed to remain for twenty-four hours. After careful removal from the chromic acid, they were placed in perforated porcelain cylinders, washed for twenty-four hours in running water, then successively transferred through a series of alcohols to 90 per cent., and into a weak solution of Bismarck brown in commercial alcohol. The roots were allowed to remain in the stain two or three days, and were then washed out for twenty-four hours in absolute alcohol, and were transferred through mixtures of alcohol and xylol and paraffin into the paraffin bath at 50° C. Six hours later they were embedded, sections cut on a Minot microtome, fixed to the slide with collodion and clove oil, cleared with turpentine and mounted in Canada balsam in oil of cajeput. This method was found to give most excellent results. The walls were deeply stained, while the protoplasm and nucleus took up the dye only sparingly. The color is especially well adapted to photomicrographic reproduction.

XIII. MEASUREMENTS AND OBSERVATIONS.

Many hundreds of sections were obtained and are still preserved. From the measurements made from them representative tables have been selected and are given below. These tables, together with the notes which follow, were made with a view to determine the changes in form and size of the cells of the convex and concave sides. In tissues of this character it is difficult to make any comparative measurements of the relative thickness of the walls. The figures represent divisions of the eyepiece micrometer and have an actual value of .002857^{mm}.

TABLE I.

Median longitudinal section of root excited geotropically for three hours and curved through an angle of 60°. The quantities are given in the nearest integer.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical						Basal		Average
(Ep)	35	30	20	50	40	42	20	43	35.
(2)	27	54	56	70	95	53	45	..	57.
(3)	54	30	30	50	30	60	..	..	42.
(4)	51	43	48	53	76	54	60	..	56.
(5)	35	35	40	40	30	38	50	30	37.
(6)	33	33	54	95	35	30	60	..	48.
(7)	30	25	30	30	28	32	36	54	33.
(8)	40	40	40	33	35	35	25	..	37.
	Average length of cells,								43.3

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal		Average
(Ep)	15	15	21	30	20	35	15	28	20	22.
(2)	22	30	18	23	27	30	25	30	23	25.
(3)	28	50	42	40	30	22	40	51	55	40.
(4)	20	25	46	43	40	30	20	45	50	38.
(5)	32	33	26	58	40	50	30	24	25	35.
(6)	18	28	28	30	40	30	20	25	20	28.
(7)	28	30	22	25	32	43	40	32	45	32.
(8)	15	25	15	18	10	35	15	20	22	19.
	Average length of cells,									29.9

TABLE II.

Tangential longitudinal section of root geotropically excited for three hours and curved through 60°. The section lay entirely within the newly formed cortex.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical							Basal		Average
(Ep)	25	23	25	45	40	25	35	46	55	35.54
(2)	30	40	50	45	55	58	60	..	..	48.3
(3)	30	50	62	60	40	37	35	..	..	45.
(4)	30	30	33	65	40	30	40	40	..	38.5
(5)	40	45	44	40	45	45	50	50	..	44.87
(6)	33	40	20	20	25	26	30	40	..	26.75
(7)	25	45	40	23	30	50	65	30	..	39.12
(8)	45	25	28	32	25	30	30	40	45	34.45
(9)	21	25	35	32	34	33	23	20	20	27.
(10)	22	22	26	30	26	30	28	30	26	26.66
(11)	30	36	16	20	22	25	23	42	38	28.
(12)	36	40	38	30	34	36	38	40	40	35.77
(13)	20	16	22	15	15	28	30	30	..	22.
(14)	20	15	20	40	36	34	34	32	..	16.37
(15)	18	30	28	22	34	34	32	34	..	29.

MEDIAN.

	Apical							Basal		Average
	25	25	20	25	24	32	28	30	..	26.2

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal		Average
(15)	25	25	30	30	35	36	38	32	..	31.37
(14)	25	21	26	20	30	26	36	35	..	26.66
(13)	..	28	30	30	31	30	26	36	28	29.87
(12)	20	10	20	11	30	10	20	35	43	21.11
(11)	35	40	30	20	30	30	20	37	37	31.
(10)	16	20	20	30	30	31	30	25	21	24.77
(9)	15	15	16	40	40	25	20	22	40	28.11
(8)	28	22	22	28	32	40	40	22	22	27.33
(7)	28	25	18	18	20	20	35	25	20	23.33
(6)	30	35	20	18	20	22	21	22	..	20.75
(5)	28	30	36	25	30	34	30	30	..	29.75
(4)	20	20	20	26	26	28	40	36	..	27.
(3)	..	..	..	..	..	..	..	..		
(2)	..	..	..	..	..	..	..	..		
(Ep)	..	..	..	..	..	..	..	..		

Average length of cells of convex side, - - - 35.45
Average length of cells of concave side, - - - 29.18

TABLE III.

Median longitudinal section of root of Zea excited geotropically three hours and curved through 60°.

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical							Basal		Average
(Ep)	12	13	14	12	12	12	13	10	10	12.
(2)	6	6	7	9	8	8	7	10	7	7.5
(3)	7	7	5	8	7	7	4	4	5	6.
(4)	7	5	6	7	11	5	9	6	8	7.
(5)	7	7	4	3	5	7	5	5	8	7.
(6)	7	7	5	4	6	6	5	7	9	6.
(7)	10	11	9	6	8	5	8	10	10	8.5
(8)	5	8	9	5	7	6	8	5	6	6.5
		Average width of cells,		-	-	-	-	-	-	7.56

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal		Average
(Ep)	12	11	12	11	10	11	11	11	..	11.
(2)	8	9	6	7	8	12	12	12	..	9.
(3)	7	8	8	9	10	9	5	5	..	9.5
(4)	7	6	5	7	4	9	10	7	..	7.
(5)	5	5	4	3	4	8	8	8	..	5.5
(6)	6	7	8	8	7	6	7	8	..	7.
(7)	10	10	9	9	9	10	8	7	..	9.
(8)	8	8	9	10	9	8	8	10	..	9.
		Average width of cells,		-	-	-	-	-	-	8.25

TABLE IV.

Table showing comparisons of average lengths of cells of convex and concave sides of root of *Zea mais*, geotropically excited for three hours and curved through 60°. The rows of cells are numbered from the epidermis toward the center of the root.

MEDIAN LONGITUDINAL SECTION.

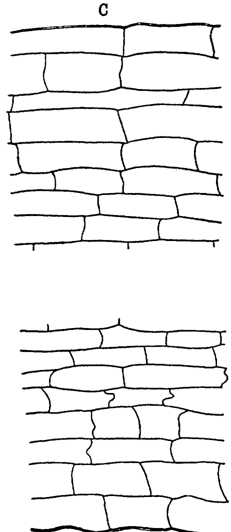
	Ep	2	3	4	5	6	7	8	9	10
Convex	35	57	42	56	37	48	33	37	..	..
Concave	22	25	40	38	35	28	32	19	..	..

TANGENTIAL LONGITUDINAL SECTION.

	Ep	2	3	4	5	6	7	8	9	10
Convex	36	48	45	38.5	44.8	26.7	39	34	27	26.6
Concave	..	..	..	27	29.7	20.7	23	27	28	24

An examination of the sections from which the above measurements were made reveals the fact that the distance from the apex of the growing point to the cross section exhibiting the shortest radius of curvature is 2^{mm}; from the apex to the beginning of the region of curvature 1.5^{mm}. At this point the root is 1^{mm} in diameter. The epidermal cells of the concave side appear densely granular. The greater number of the nuclei in the cortex of the concave side appear to lie on the peripheral side of the cells, though not always substantiated by actual count. The axial diameter of the cortical cells is smaller than that of the convex side, though no great compression has been exerted in this plane, since no foldings were observable in the longitudinal walls. The radial cross walls were of a contour indicative of compression in an axial direction and exhibited a wavy or undulating outline (*fig. 5*).

C



A

FIG. 5. Longitudinal sections through curved portion of a root of Zea three hours after excitation. *C*, convex side; *A*, concave side (see tables I–IV).

TABLE V.

Median longitudinal section of root of *Zea mais* twenty hours after excitation began, and after a curvature of 105° had been effected.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical							Basal		Average
(Ep)	90	40	50	60	120	55	..	..	..	69.2
(2)	70	40	60	55	90	125	..	..	..	73.3

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE—*cont'd.*

	Apical								Basal	Average
(3)	35	30	40	48	55	52	40	..	..	42.9
(4)	38	38	30	60	80	70	50	..	..	52.3
(5)	55	33	42	70	50	45	..	..	..	49.2
(6)	48	30	30	40	40	35	..	..	..	37.2
(7)	30	32	32	33	23	45	25	..	..	31.4
(8)	23	20	25	35	30	35	34	..	..	28.9
	Average length of cells, - - - - - -									48.05

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical									Basal	Average
(Ep)	23	20	20	30	18	30	15	20	10	10	19.6
(2)	14	22	20	20	30	16	20	12	10	25	18.9
(3)	20	20	26	35	23	38	35	30	25	37	29.3
(4)	..	..	23	30	32	35	31	30	30	40	28.8
(5)	..	..	..	..	..	23	18	20	20	15	19.2
(6)	35	30	28	27	20	20	23	18	..	..	25.2
(7)	34	37	30	35	28	31	30	31	..	..	31.9
	Average length of cells, - - - - - -										24.7

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal	Average
(Ep)	9	9	9	8	10	9	10	10	9.25
(2)	8	8	5	5	8	8	7	7	8.25
(3)	7	6	6	6	8	8	7	5	6.62
(4)	5	5	4	5	7	8	11	11	7.
(5)	10	10	10	11	14	12	12	10	11.1
(6)	19	14	19	15	14	14	15	16	15.75
(7)	20	22	23	22	20	21	22	..	21.43
	Average width of cells, - - - - - -								11.4

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical								Basal	Average
(Ep)	8	8	5	6	5	3	5	3	5	5.77
(2)	6	8	8	7	7	8	7	7	7	7.22
(3)	5	5	3	5	4	5	5	5	5	4.66
(4)	5	6	6	6	8	6	6	8	7	6.44
(5)	10	9	9	6	6	4	5	7	7	7.22
(6)	5	4	5	4	6	4	5	9	7	5.44
(7)	9	10	11	10	10	10	10	10	9	9.98
(8)	10	9	10	7	10	9	9	8	10	9.11
	Average width of cells, - - - - - -									6.98

TABLE VI.

Comparison of measurements of rows of cells in median longitudinal section of root of Zea excited geotropically for twenty hours and curved through 105°.

MEASUREMENTS OF LENGTH.

	Ep. 1	2	3	4	5	6	7	Average
Concave	19.6	18.9	29.3	28.8	19.2	25.2	31.9	24.7
Convex	69.2	73.3	42.9	52.3	49.2	37.2	31.4	48.05

MEASUREMENTS OF WIDTH.

	Ep. 1	2	3	4	5	6	7	Average
Concave	9.25	8.25	6.62	7.	11.1	15.7	21.4	11.4
Convex	5.77	7.22	4.66	6.4	7.2	5.4	9.8	6.98

An examination of the sections of which measurements are given in tables V and VI shows that the distance from the apex of the growing point to the cross section having the shortest radius of curvature is 2.24^{mm}, and the width of the motor zone at its forward edge is 1.12^{mm}. The length of the cells from which the annular vessels will be formed is about two-thirds of that of these cells in a region at a distance of 1.5^{mm} in a basal direction from the region of greatest curvature.

The granular density of the protoplasm of the epidermal cells of the concave side is less marked than in younger curvatures, and the external walls are thickened two to four times their former diameter. Root hairs are abundant on the regions both apical and basal to the region of greatest curvature, but are also wholly absent from the region exhibiting the shortest radius of curvature, when the walls are most thickened. The sub-epidermal cells are rectangular in outline, with the end walls slightly oblique and exhibiting undulating foldings. The rows of cells in the fourth to the eighth layers have taken a contour indicative of axial compression. The axial walls bulge in a radial

direction, and the radial walls are folded more sharply than those of the layers near the epidermis, or in the same region in younger curvatures. The difference in the granular densities of the cortical regions of the convex and concave sides has nearly disappeared. However, the membranes of the entire concave side have become much heavier. The epidermal cells of the convex side, as well as the underlying two or three layers, have evidently undergone passive stretching. The longitudinal walls have been brought closer together, and in some instances the appearance of collapse is present. The end walls of the epidermal cells are distorted obliquely, but on account of their greater thickness do not exhibit the sharp foldings of the subepidermal layers. The inner layers of the cortical region have rounded turgid outlines, and the curves of the walls are wavy in outline, indicating that these cells have been most active in producing the elongation of this side of the organ. Intercellular spaces are larger and more abundant than in the concave side.

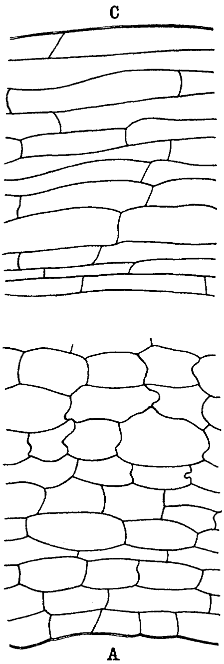


FIG. 6. Longitudinal sections through curved portions of root of Zea twenty hours after the beginning of excitation. *C*, convex side, *A*, concave side (see tables V–VI).

The apical portion of the root, 1.2^{mm} in length, has become quite straight, and the tip no longer exhibits traces of the strain exerted upon it by the curving forces when the motion began. The forward limit of the region of curvature is quite sharply marked (*fig. 6*).

TABLE VII.

Median longitudinal section of *Zea mais*, placed vertically upright and curved through 160°. The measurements were made in that portion of the root in which the first geotropic excitation occurred, and this part of the curvature was seventy hours old, and exhibits an angle of 90°.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical							Basal	Average
(Ep)	50	55	60	42	30	20	35	40	45	53.1
(2)	100	40	75	75	115	110	..	..	..	64.38
(3)	70	90	80	120	145	85	110	140	..	105.
(4)	70	70	80	140	110	100	70	100	..	92.5
(5)	110	80	90	50	150	80	90	60	..	88.88
(6)	100	120	45	80	60	110	..	..	..	92.5
(7)	70	70	80	70	70	80	..	..	..	73.3
(8)	65	50	70	80	45	50	..	..	..	60.
	Average length of cells -									78.75

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

(Ep)	23	22	16	22	16	28	16	..	..	20.4
(2)	43	40	42	40	40	38	40	..	..	40.55
(3)	40	40	65	50	52	48	65	..	..	51.4
(4)	34	34	30	40	40	47	51	..	..	39.7
(5)	32	30	30	51	45	40	50	..	..	39.7
(6)	32	30	45	46	47	35	45	..	..	40.
(7)	38	30	30	45	40	35	35	..	..	36.1
(8)	36	30	20	32	52	41	32	..	..	34.7
	Average width of cells, -									25.28

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal	Average
(Ep)	11	10	12	11	13	10	11	11	11	11.1
(2)	6	11	7	8	10	10	11	9	11	9.2
(3)	5	8	9	6	5	15	13	13	10	8.2
(4)	11	10	15	11	11	11	10	8	9	10.6
(5)	10	18	15	15	15	14	12	11	18	14.2
(6)	14	14	12	11	15	16	18	18	20	15.3
(7)	20	15	20	14	14	15	20	18	12	16.4
(8)	18	18	15	16	13	12	15	16	14	15.2
	Average width of cells, -									12.52

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

(Ep)	9	8	11	8	8	9	8	9	7	8.55
(2)	10	11	9	11	10	8	7	8	9	9.22
(3)	9	9	8	7	7	9	7	6	7	7.77
(4)	7	9	8	6	8	7	7	5	7	7.11
(5)	8	10	10	10	9	15	14	15	15	11.77
(6)	16	10	8	10	10	13	12	14	11	11.
(7)	12	11	9	10	11	14	14	17	16	12.66
(8)	10	11	10	10	14	14	12	15	15	12.33
	Average width of cells, -									10.05

The width of the sections from which above measurements were taken is 1.12^{mm}; the width of the cortex (including the epidermis) of the concave side is .4^{mm}, and of a similar region on the convex side .3^{mm}. The mechanics of cells are to be compared with the data given in tables I to V, since the amount of curvature is not much greater. The differences are to be ascribed to changes brought about by growth subsequent to curvature.

The epidermal and sub-epidermal cells of the concave side are more densely granular than those of the convex side. The emergences from the epidermal system are very few, and the walls of all of the cells show a thickening noticeably greater than those of the convex side. The foldings of the end walls seen in the sections described in the preceding tables are not to be found here. On the other, the end walls of the cells of the convex side exhibit more sharply folded bends than those described in tables V–VII. The epidermal cells exhibit a normal number of emergences, as well as the flanks of the organ. The epidermal and sub-epidermal walls do not show the evidences of the tensions to be seen in younger curvatures, and the suggestion arises that these tensions may have been in part relieved by growth subsequent to curvature. This growth would follow, of course, the laws governing growth under tensions, by which the first accession of strains would retard elongation, to be followed later by an accelerated elongation, which would obliterate evidences of tension.

TABLE VIII.

Median longitudinal section of root of *Zea mais* geotropically excited and curved through 90°. Portion of root containing curvature killed after tip had reached a distance of 3^{cm} from the cross section having the shortest radius of curvature.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical					Basal	Average
(Ep)	..	..	..	..	..	..	....
(2)	90	65	45	130	100	100	88.3

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE—*cont'd.*

	Apical					Basal	Average
(3)	100	80	90	125	110	90	97.5
(4)	80	85	85	95	75	80	83.3
(5)	54	42	52	50	50	45	48.8
(6)	60	65	65	70	55	70	64.1
(7)	54	60	65	75	80	75	68.1
(8)	60	80	50	60	65	75	65.
(9)	65	45	60	65	70	60	68.
	Average length of cells,		-	-	-	-	71.99

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal		Average
(Ep)	..	..	..	..	..	..	..	..	..	
(2)	..	..	..	..	..	..	..	..	..	
(3)	50	28	30	52	42	50	45	55	..	44
(4)	25	15	20	32	30	50	30	50	..	31.5
(5)	45	20	35	25	30	40	50	25	..	33.75
(6)	30	40	25	52	52	40	45	..	..	38.62
(7)	30	45	35	32	42	50	52	..	..	40.85
(8)	30	45	30	35	45	50	60	..	..	42.14
(9)	50	45	52	40	48	35	30	..	..	43.57
	Average length of cells,			-	-	-	-	-	-	45.

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical							Basal	Average
(Ep)	..	..	..	..	..	..	..	..	....
(2)	..	..	..	..	..	..	..	..	....
(3)	..	..	..	..	..	..	..	..	....
(4)	9	7	6	8	8	8	6	5	7.12
(5)	7	7	6	9	6	6	8	7	7
(6)	7	6	6	7	7	8	8	8	7.12
(7)	8	8	9	7	9	11	7	9	8.5
(8)	7	7	9	7	8	8	10	7	7.89
(9)	9	9	8	8	7	9	7	9	8.25
(10)	10	10	11	10	9	10	11	12	10.43
(11)	11	12	13	13	13	12	11	..	12
	Average width of cells,			-	-	-	-	-	8.53

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal	Average
(Ep)	..	..	..	..	..	..	..	..	....
(2)	..	..	..	..	..	..	..	..	....

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE—*cont'd.*

	Apical							Basal	Average
(3)	..	..	..	..	..	..	..	..	....
(4)	8	6	7	6	7	7	6	..	6.71
(5)	8	7	8	8	7	6	7	..	7.42
(6)	12	11	11	11	11	12	13	..	11.57
(7)	15	15	15	15	15	12	13	..	14.28
(8)	17	16	15	15	15	15	16	..	15.57
(9)	14	15	11	10	11	12	10	..	11.82
(10)	15	15	15	15	15	11	16	..	14.57
			Average width of cells,		-	-	-	-	11.69

The curvatures from which the above table was made are comparable to those described under tables I–IV. The angle of curvature is approximately the same, and growth for one hundred hours following the curvature has ensued. After the lapse of this period, the entire surface of the curved portion is free from root hairs. In addition to the disintegration of the walls of the root hairs, the external cells of the root have died. In the sections examined the epidermal and two underlying layers of the concave side, and the epidermal and one layer on the convex side have collapsed. The total width of the section is 1.04^{mm}, of the cortical region of the concave side $.342^{mm}$, of the convex side $.24^{mm}$, and of the central cylinder $.458^{mm}$. The foldings of the end walls of the cells of the concave side have almost disappeared, and present a gently undulating outline, while those of the convex side are pronounced, exhibiting U or V outlines. In all of the curvatures of this stage of development initial layers of secondary roots were to be found on the convex side of the cylinder only. In the above section the rudimentary root had pierced two or three layers of the cortical cells. This is in accordance with the facts described by Noll, in which secondary roots were found to spring from the convex side of curving radicles only. While the initial cause of such an arrangement is not apparent, it is very easily seen that the formation of branches on the concave side of the organ would not only entail the expenditure of many times as much energy in piercing the compressed cortex, but the tensile strength of the curved portion

would be decreased. This latter effect is absent from an arrangement of the branches on the convex side, and the fixative power of the system is increased.

TABLE IX.

Median longitudinal section of root of *Zea mais* bent mechanically through 90°.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical						Basal	Average
(Ep)	54	35	50	40	..	85	90	50.5
(2)	90	90	85	120	100	165	110	95.
(3)	125	75	95	100	130	65	65	93.5
(4)	60	100	55	75	70	70	80	73.
(5)	60	90	100	80	60	80	80	79.3
(6)	60	75	45	80	60	95	85	71.3
(7)	45	55	80	60	70	60	90	65.5
(8)	65	55	60	70	60	70	50	61.4
	Average length of cells,			-	-	-	-	73.56

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical					Basal	Average
(Ep)	55	45	45	20	60	50	45.8
(2)	60	60	65	30	100	45	60
(3)	60	75	28	50	26	70	51.5
(4)	..	..	75	75	50	65	66.4
(5)	70	50	75	50	65	70	64.2
(6)	65	65	70	55	95	..	52.5
(7)	75	60	63	54	80	50	63.7
(8)	50	50	50	60	50	50	50.7
	Average length of cells,			-	-	-	56.85

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical							Basal	Average
(Ep)	7	6	7	..	5	6	6	7	6.5
(2)	7	7	7	7	11	9	7	8	8.
(3)	4	7	8	9	5	5	5	5	6.
(4)	7	6	8	8	7	6	7	5	6.5
(5)	6	6	7	7	6	8	8	8	7.
(6)	6	7	6	6	7	8	6	9	6.87
(7)	8	8	10	9	7	8	7	..	8.14
(8)	5	6	7	9	7	7	..	..	6.83
	Average width of cells,			-	-	-	-	-	6.98

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical							Basal	Average
(Ep)	8	7	8	6	5	7	7	8	7.
(2)	9	9	9	10	9	10	10	9	9.375
(3)	9	8	6	8	6	6	11	10	8.
(4)	10	9	8	8	9	7	9	9	8.62
(5)	7	8	8	8	9	11	10	..	8.71
(6)	9	8	8	8	7	8	10	11	8.62
	Average width of cells,	-			-	-	-	-	8.4

The root treated in the above manner offers a sequel to Noll's bending experiments, by which the ductility of the walls of the concave side of the stems was found to be diminished, or less than the normal. The region of curvature artificially produced coincided with that of geotropically excited roots, but it extended over the entire growing region of the tip in such manner that the extreme apical portion was bent only by the strains exerted upon it by the curvature artificially produced in the growing region. This fact disposes of the theory of Sachs that the entire apical portion is active in curvature. The region of shortest curvature in all of these experiments was found to be about 2^{mm} from the tip of the apical region, and the curvature decreased quite gradually apically and basally, as is asserted of the root in geotropic curvatures by Sachs. The form of such curvatures is undoubtedly due to the distribution of ductility in the different portions of the organ and the resultant curve approaches a hyperbola. In geotropic curvature the greatest bending occurs within very narrow limits in such manner as to favor the assumption that an increase in the ductility of the membranes has taken place here.

The cortical region of the convex side has a width of $.24^{mm}$, and of the concave side $.25^{mm}$, the central cylinder $.4^{mm}$.

The measurements given above show that actual enlargement of the superficial content of the cells of the convex side, and a diminution of those of the concave side has taken place, yet there is no apparent difference in the density of protoplasmic contents. The cells of the concave side exhibit plainly marked evidence of the compression which has been exerted upon them.

Some are thrown from a position parallel to the longitudinal axis of the root and the end walls exhibited foldings, shallow and V shaped, but in no place do these elements exhibit the contours to be seen in curvatures of 90° produced by geotropic excitation, where the radial and longitudinal axes were often equal. The epidermal cells of the convex side were torn and collapsed in places. The longitudinal walls of all cells on this side were thrown outward and inward from their natural positions. The end walls were sharply and deeply folded and pouched.

The greater distortion of the cross walls on both sides of the organ is to be attributed in part to the fact that these membranes are quite newly formed and have not acquired a rigidity which enables them to withstand columnar strains of any amount. With the growth of the cortex of the concave side in thickness, the foldings in these walls are taken up in part or almost wholly in slight curvatures.

TABLE X.

Median longitudinal section of root of *Zea mais* geotropically excited for one hour, and then mechanically in the plane of would be curvature through 90°.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical						Basal		Average
(Ep)	48	40	35	85	35	40	40	38	45.75
(2)	30	75	42	40	20	30	80	120	50.9
(3)	45	40	40	50	50	80	50	80	54.4
(4)	75	70	35	42	45	45	30	40	47.75
(5)	55	40	20	50	45	30	30	50	40.
(6)	50	21	23	25	40	42	40	58	37.38
(7)	42	32	36	30	35	45	40	40	37.5
(8)	40	40	30	45	50	42	45	55	43.37
	Average length of cells,			-	-	-	-	-	44.63

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical						Basal		Average
(Ep)	14	25	14	20	20	80	20	50	17.25
(2)	30	21	20	35	50	54	48	45	37.87
(3)	30	22	24	42	20	20	36	52	30.75
(4)	18	20	20	20	42	22	30	18	23.75

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE—*cont'd.*

	Apical							Basal	Average
(5)	28	28	25	22	22	26	30	18	23.62
(6)	28	25	25	30	30	28	20	20	25.75
(7)	20	20	23	31	30	30	35	40	28.62
(8)	28	22	40	20	28	35	33	36	30.25
(9)	20	20	28	38	22	30	20	20	24.75
	Average length of cells,	-	-	-	-	-			30.32

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical										Basal	Average
(Ep)	7	8	8	6	6	6	6	6	6	5	6	6.36
(2)	5	4	5	4	4	4	4	5	5	5	5	5.55
(3)	5	5	5	..	4	..	..	..	..	..	..	4.75
(4)	7	7	8	..	10	9	7	8	9	7	5	8.
(5)	12	10	10	..	10	10	10	9	11	9	..	10.1
(6)	8	9	9	..	10	10	10	11	10	9	..	9.66
(7)	10	13	12	11	10	10	10	10	10	10	..	10.6
(8)	8	9	8	..	8	7	8	9	9	..	..	8.25
			Average width of cells,	-	-	-	-	-	-			7.91

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical								Basal	Average
(Ep)	11	10	11	10	8	8	10	..	..	9.7
(2)	10	10	11	13	14	7	8	8	..	10.1
(3)	7	7	5	..	6	8	8	9	..	7.1
(4)	7	9	9	7	7	8	8	9	..	8.
(5)	7	8	8	8	8	10	9	10	10	8.66
(6)	6	8	7	11	12	12	12	13	..	10.1
(7)	12	11	12	6	8	9	9	..	..	9.55
(8)	12	12	12	11	12	11	10	11	10	11.22
		Average width of cells,	-	-	-	-	-			9.3

The total width of the section in the region of curvature is about .82^{mm}, of the convex cortical region .22^{mm}, and of the concave cortical region .2^{mm}. The walls of the epidermal cells of the concave side are wavy and folded, showing the end pressure exerted against them. The cortex of the concave side exhibits numerous foldings on both longitudinal and end walls, much greater than in the cells mechanically bent without previous excitation. The epidermal and three (in some places four) sub-

epidermal layers are torn and collapsed, and the cortex shows the ordinary foldings of the end walls much more marked than those of the mechanically bent organ. On the whole, the curvature of the organs geotropically excited is not distributed over so great a region as in those bent mechanically from a normal condition. This might of course be due to a smaller coefficient of turgidity, and the recurrence of this relation through all of my experiments leads to the suggestion that some alteration must have taken place in the membranes to permit the localization of the curvature. Furthermore, it is impossible to account for the excessive folding and wrinkling of the walls of the cells of the concave side, with decrease of the resistance of the membranes of the convex side, as due to stretching. This decrease would allow a greater part of the bending force to act as a compression upon the cortex of the concave side.

TABLE XI.

Median longitudinal section of normal root. The measurements included a region beginning at a distance of 2^{mm} from the tip of the growing point and of the same age and stage of development as the curved portion of the root described under table V.

MEASUREMENTS OF LENGTH OF CELLS OF SIDE A.

	Apical							Basal	Average
(Ep)	7	8	7	11	7	8	7	10	10	9.37
(2)	16	12	12	10	21	20	12	12	30	16.
(3)	12	11	16	10	14	15	11	21	16	15.75
(4)	21	11	20	11	14	14	10	12	15	16.
(5)	12	11	18	10	12	10	12	18	16	14.88
(6)	15	16	16	16	12	18	18	17	16	16.75
(7)	10	10	16	20	16	15	15	10	10	15.25
(8)	11	12	18	10	11	17	18	10	10	14.62
		Average length of cells,								14.82

MEASUREMENTS OF LENGTH OF CELLS OF SIDE B.

	Apical						Basal	Average
(Ep)	10	7	8	6	6	11	6	6	7.5
(2)	11	10	9	18	14	25	12	15	15.12
(3)	10	8	10	9	12	21	7	8	10.62
(4)	10	11	14	12	10	12	10	10	11.12

MEASUREMENTS OF LENGTH OF CELLS OF SIDE B—*cont'd.*

	Apical							Basal	Average
(5)	10	7	12	21	13	12	11	11	12.12
(6)	11	10	12	11	14	12	11	14	11.88
(7)	9	10	11	12	13	14	10	12	11.25
(8)	10	10	11	12	13	10	13	12	11.25
	Average length of cells,	-	-	-	-	-			11.35

MEASUREMENTS OF WIDTH OF CELLS OF SIDE A.

	Apical							Basal	Average
(Ep)	10	10	10	10	9	9	9	10	9.6
(2)	7	8	8	8	7	7	7	8	7.5
(3)	7	7	7	5	5	6	5	5	5.87
(4)	7	7	6	6	7	6	6	5	6.25
(5)	10	10	10	10	10	10	12	11	10.37
(6)	10	10	10	10	10	11	10	10	10.12
(7)	9	10	8	7	6	7	7	8	7.75
(8)	10	9	8	9	9	9	8	9	8.87
	Average width of cells,	-	-	-	-	-			8.29

MEASUREMENTS OF WIDTH OF CELLS OF SIDE B.

	Apical							Basal	Average
(Ep)	10	8	8	8	9	11	11	11	9.5
(2)	8	8	9	9	8	9	9	9	8.62
(3)	6	7	7	7	7	8	8	9	7.37
(4)	8	9	9	10	10	6	7	8	8.25
(5)	10	7	8	6	9	10	9	8	8.37
(6)	7	8	7	9	9	8	8	10	7.37
(7)	6	7	6	5	5	6	5	5	5.62
(8)	9	9	10	9	10	10	9	8	9.25
	Average width of cells,	-	-	-	-	-			8.047

Measurements of the cells, to obtain the normal stature of the cells of the root for comparison with those of the convex and concave sides, were made by Cieselski upon the portion apical to the curvature (see quotation on p. 328.)

By this method, the average length of the normal cells was found to be .099^{mm}, of cells of the concave side .02^{mm}, of cells of the convex side .125^{mm}. These figures were obtained from roots in which the curvature had been left some distance behind by the growing point, and the original proportions between the length

of the cells of the normal and curved portions had been distributed by the subsequent growth, which is of course modified by the tension set up by curvature. Sachs raised the objection that Cieselski's method concealed the true relations of the length of the cells of the convex side to the normal, and that the excessive growth of the former was not apparent. In an effort to evade this error, Sachs compared the length of the cells of the curved portion with averages attained from the measurement of from twenty to forty cells in regions apically and basally to the curvature.

According to his own account, the apical portion of the root was allowed to obtain a length of 2 to 3^{cm}, and the basal portion had made its full growth. He deemed it desirable to allow the curved portion to make the sharpest angle possible, and to reach a great thickness. It is evident that his results do not show the relative stature of the cells of the two sides at the time of curvature, since the subsequent growth processes have intervened. His figures are therefore strictly comparable to those given by myself in table VIII, made from curvatures three to five days old. Sachs found that the average length of cells of the root of *Vicia Faba*, apical and basal to curvatures, was 40 to 44 respectively, with a general average of 42. The length of cells of the convex side was 41, and of the concave side 26.3. In a second example the lengths of the apical and basal portions were found to be 23.2 and 26.2, with an average of 24.6. The average length of cells of the convex side was 28.3, and of the concave side 15. In a root of *Æsculus Hippocastanum* the average lengths of the apical and basal portions were found to be 16 and 23, that of the cells of the convex side 27, and of the concave side 13.3. In a second example of this species the lengths of the cells of the apical and basal portions were found to be 19 and 21.2, with an average of 20.1. The average length of cells of the convex side was 28.1, and of the concave side 9.3. The figures given by Sachs represent divisions of the micrometer of a value of $.005^{mm}$.

The fact that the average length of the cells of the convex

side was found to be less than that of the average length of the normal cells in many examples beside those quoted led Sachs to the conclusion that the discrepancy was due to faults in observation. The fault is in the system of obtaining the measurements, however. If only the same factors were operative in the production of curvature that are to be found in normally elongated roots, this method of obtaining the average stature of the normal cells would be allowable. This is not the case, however, as the curvature is produced by an excessive elongation of the convex side, which might be due to growth or ductile stretching, but in either case would be followed by after effects that would destroy the normal relations. Even if this system of measurements were applied to forming or newly formed curvatures, the rapidly increasing and unequal rate of growth of the motor zone would destroy the proportions of the average. A glance at the tables given above shows that the increase in the length of the cells in the basal direction is by no means uniform.

In order to obtain the stature of normal cells in my own observations the measurements were made upon a region corresponding in distance from the apex and stage of development with the curvatures with which comparison was to be made. This region, from which the data in table XI were obtained, corresponds to the region of curvature of the root curved through 105° (see table V). Identical methods of preparation were used and the cells measured from a radial longitudinal plane eight cells in length and eight cells in width radially.

In a comparison of the data obtained from the normal root with the figures of a root curved through 105° after twenty hours of geotropic excitation (table V), the following facts are to be noted. The average lengths of the cells of the normal root are 11.35 and 14.82. The average length of the cells of the concave side in the root bent at an angle of 105° after twenty hours' excitation is 24.7, and of the convex side is 48. If it is supposed that the error has been made in measuring the region in the normal root nearer the tip than in the curved root, the lengths of the cells in the curvature of a root three hours

after excitation (concave 29, convex 43) show that in Zea an elongation of both sides of the root takes place during curvature. It is apparent, however, that the epidermal and sub-epidermal cells, which have been in a state of passive tension previous to curvature, will show purely mechanical changes. These mechanical changes will depend upon the angle and rapidity of curvature as well as upon the thickness of the root. It is possible that the passively stretched tension of the epidermal cells in young roots may be converted into a compressed tension in older organs.

A comparison of the radial diameters of the cells of the two sides exhibits changes of a similar nature. The radial diameters of the cells of the convex sides of roots steadily decrease in Zea as the angle of curvature increases, while the reverse is true of the concave side. The decrease is most marked in the peripheral layers of the convex side, and the cortical layers of the concave side in Zea. The radial diameter of the convex side in table III is 7.56, in table VI 6.98. The average diameter of the cells of the concave side in table I is 8.25, in table VI is 11.4.

It seems well demonstrated that the extension in the length of the cells of the convex side of the root of Zea is accompanied by a decrease in radial diameter, and that the slight elongation of the cells of the concave side is attended by an increase in radial diameter. Such conditions lead to the conclusion that the elongation of the convex side is a ductile extension of the longitudinal walls. The ductile extension is accompanied by the usual amount of growth. The longitudinal compression of the cells of the concave side permits only a minimum of growth in this direction and facilitates extension in a radial direction.

TABLE XII.

Median longitudinal section of root of *Zea mais*, allowed to curve geotropically six hours and then reversed five hours. The measurements are taken from the portion of the old curvature, which had decreased from 40° to 15°. The new curvature was formed at a distance of 2^{mm} apical from the first curvature.

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical						Basal		Average
(Ep)	80	70	60	30	50	60	..	..	56.6
(2)	100	80	90	46	30	90	..	..	72.6
(3)	50	50	70	35	45	60	..	..	51.6
(4)	70	35	40	50	50	50	..	..	46.1
(5)	70	60	30	60	50	50	..	..	53.3
		Average length of cells,			-	-	-	-	56.04

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical					Basal		Average
(Ep)	50	70	100	70	90	..	..	76.
(2)	60	60	40	45	60	..	..	53.
(3)	60	55	50	48	50	..	..	52.6
(4)	70	45	44	32	35	..	..	48.4
(5)	60	50	90	40	35	..	..	55.
(6)	50	55	65	65	34	..	..	53.8
		Average length of cells,			-	-	-	57.7

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical						Basal		Average
(Ep)	4	4	3	..	3	4	..	..	3.6
(2)	6	7	7	7	5	5	..	..	6.1
(3)	10	9	9	7	5	5	..	..	7.5
(4)	9	8	10	9	9	7	..	..	8.6
(5)	10	11	10	9	10	10	..	..	10.
			Average width of cells,			-	-	-	7.16

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical						Basal		Average
(Ep)	2	3	2	3	2	3	..	..	2.5
(2)	7	5	5	8	5	5	..	..	6.
(3)	6	6	8	9	7	8	..	..	7.3
(4)	6	7	7	7	8	10	..	..	7.5
(5)	5	7	9	10	10	10	..	..	8.5
(6)	11	12	13	11	11	10	..	..	11.3
			Average width of cells,			-	-	-	7.18

The data given in the above table show that whatever inequality has been present in the curved portion of the root during the first stage of curvature the subsequent processes have reduced this inequality to a minimum. The greater length of the cells of

the concave side may not be held to have special significance, since similar inequalities are to be found between the sides of normal roots. The width of the cells of both sides is below the normal, and by no means sustains the proportions to the length to be found in other curvatures. This can be due only to the fact that both sides in succession have been subjected to a ductile stretching, and that the extension of the cells may not be taken up, but is irreversible after the lapse of five hours. The processes of growth then follow the extension of the membranes within this period. The foldings of the walls in the above sections are not especially marked.

TABLE XIII.

Median longitudinal section of root of *Phoenix dactylifera* geotropically excited twenty hours and curved through 90°.

MEASUREMENTS OF WIDTH OF CELLS OF CONVEX SIDE.

	Apical							Basal	Average
(Ep)	8	9	8	7	7	7	7	7	7.5
(2)	10	9	8	6	7	8	8	7	7.8
(3)	5	5	5	7	5	6	5	5	5.4
			Average width of cells,				-	- -	6.9

MEASUREMENTS OF WIDTH OF CELLS OF CONCAVE SIDE.

	Apical						Basal		Average
(Ep)	10	10	8	8	8	8	7	..	8.4
(2)	9	10	8	9	10	8	9	..	9.
(3)	7	7	7	6	5	5	6	..	6.1
			Average width of cells,			-	-	- -	7.8

MEASUREMENTS OF LENGTH OF CELLS OF CONVEX SIDE.

	Apical						Basal		Average
(Ep)	8	9	10	7	7	7	7	..	8.
(2)	10	12	11	15	13	15	13	..	12.7
(3)	15	15	10	15	15	20	20	..	15.7
			Average width of cells,			-	-	- -	12.1

MEASUREMENTS OF LENGTH OF CELLS OF CONCAVE SIDE.

	Apical						Basal		Average
(Ep)	3	2	2	2	2	3	2	..	2.3
(2)	5	6	3	3	4	5	8	..	4.8
(3)	7	7	7	6	5	4	3	..	5.5
			Average length of cells,			-	-	- -	4.2

TABLE XIV.

Median longitudinal section of *Phoenix dactylifera*, same as table XIV. The region from which measurements were made was halfway between the endodermis and cortex. The rows of cells apparently of maximum size were measured.

MEASUREMENTS OF CELLS OF CONCAVE SIDE.

Length	9	5	6	4	5	5	4	7	9	9
		Average length,			-	-	-	-	-	- 6.3
Width	12	13	12	11	13	12	12	10	11	10
		Average width,			-	-	-	-	-	- 11.5

MEASUREMENTS OF CELLS OF CONVEX SIDE.

Length	20	18	20	17	18	20	21	18	12	15
		Average length,			-	-	-	-	-	- 17.9
Width	20	20	20	14	15	12	13	12	13	13
		Average width,			-	-	-	-	-	- 15.2

The curvatures of Phoenix offer distinct variations from those of Zea, of which the most striking is the extensive development of the cortex on the convex side of the root.

The width of the layer external to the stele on the convex side is 30 and on the concave side 25. This difference is shown also by the measurements of the individual layers of cells. The radial diameters of the epidermal and sub-epidermal cells of the concave side are slightly in excess of those of the convex side, but it may be seen very plainly that the changes in these cells are purely passive and mechanical. The differences between the longitudinal diameters of these cells are of course in favor of those of the convex side, and the changes in form of the cells of these layers are almost exactly in imitation of the folds of the bellows of an accordion.

The force operative in producing curvature is to be found in the cortical cells between the fifth and sixth layer from the epidermis and the endodermis, and whatever the nature of the changes involved, it is found that an extension of the cells of the convex side in both a radial and longitudinal direction occurs.

It is important to note that this is the first establishment of the fact that the radial diameter of the convex side of any root becomes greater than that of the concave side. Cieselski affirmed the same fact concerning Zea, Phaseolus, and Pisum in 1871, but it was disproven by Sachs a year later, and recently by myself in the same plants. It had come to be regarded, therefore, as a well founded fact that the radial diameters of the convex sides of stems increase during curvature and those of roots decrease, and that while the longitudinal diameters of the cells of the convex side of roots increased the radial diameters did not change or decrease, while exactly the reverse conditions were to be found in the concave side.

It is noteworthy in this connection that the roots offering similar conditions to stem curvatures exhibit similar reactions, and it seems reasonable to conclude, therefore, that since the morphological character of the tissues involved is not always identical, this similarity in behavior is founded upon mechanical necessities. Furthermore, it is to be said that the roots of Phoenix offer unmistakable evidence of the shortening of the concave side.

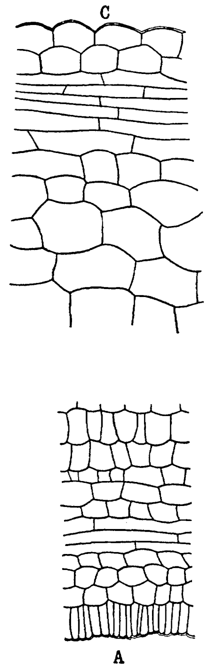


FIG. 7. Median longitudinal section of curved portion of root of *Phoenix dactylifera* twenty hours after the beginning of excitation. *C*, convex side; *A*, concave side (see tables XIII, XIV).

XIV. INTERPRETATION OF EXPERIMENTAL RESULTS.

The most important question involved in the solution of the various problems connected with curvature is the determination of the nature of the changes involved in the extension of the cells of the convex side of the organ, to ascertain whether the elongation of the membranes is due to the actual intussusception of new material, or whether the membranes undergo induced

changes of elastic extensibility, which finally becomes converted into ductility. The last method has been somewhat conclusively demonstrated by Noll in stems (16). The chief evidence upon which this conclusion rests consists in the fact that the epidermal and collenchyma cells of the convex side show an enlargement of three diameters during curvature, and that the enlargement is accompanied by a decrease in the thickness of the cell walls. Not only are the membranes of the convex side thinner than those of the concave side, but they are thinner than those of normal tissues of the same stage of development. The extension is also accompanied by changes in the qualities of the membranes, as shown by refraction and reaction of staining fluids.

In the application of the same tests to the curvatures of roots some difficulty is encountered on account of the relatively small thickness of the walls; furthermore, the different condition of the tissues must be taken into account. In stems the epidermis and collenchyma are in a state of active growth which may be maintained for a long period, and these layers may elongate during curvature with a rapidity equal to that of the cortex, and they may not; in the latter instance they will experience stretching tension from the cortex. In roots, on the other hand, the epidermal and sub-epidermal layers are not in a state of rapid elongation, but have attained the greater part of their growth; furthermore, these cells are capable of active enlargement during a period of one or two days at most, and are then cast away. In consequence of this fact the peripheral layers of cells undergo a passive stretching on the convex side which increases the axial and decreases the radial diameter. The reverse is true of the concave side. The underlying layers of cortex in Zea undergo an axial extension in the convex side, and a radial extension of the concave side. Alterations in the radial diameter of the first and the axial diameter of the second are not exactly ascertained, but the amount of change must be very slight. The roots of Phoenix have a much greater relative thickness than those of Zea, and are furnished with a layer of sclerenchymatous tissue

underneath the epidermal layers. The epidermal system exhibits similar reactions to those of Zea, except that the changes are relatively greater than in Zea, due no doubt to the greater thickness of the root and the consequent greater distance of the epidermis from the central cylinder. The arms of the lever extending from the periphery of the concave to the convex side would be twice as long as that of Zea. The above differences are mechanical, but the cortex of Phoenix also offers distinct differences in behavior from that of Zea. The axial diameter of the cells of the concave side has not increased, and is not greater than that of the same region apical to the curvature. The increase of the radial diameter has been very slight. The cells of the cortex of the convex side have increased in radial as well as axial diameter, in a manner similar to that in stems as described by Kohl (12), and by Noll (17). It is difficult to account for the similarity of the behavior of the curvatures of roots of Phoenix and dicotyledonous stems, except as a concomitant of the mechanical structure, though the real necessities are not apparent.

Differences in the quality of the membranes are not so easily distinguished in young roots as in old stems. The sections of the roots of Zea which have been excited geotropically for three hours and stained in Bismarck brown exhibit slight differences between the cortex of the convex and concave sides. Those of the concave side have taken the stain more deeply and are thicker than those of the convex side. After remaining forty-eight hours in alcohol the membranes of the convex side appear only slightly tinted and are not so highly refractive as those of the concave side, which are still more deeply colored. These results do not bear strict comparison with the reactions of stems, since the action of the agents used in killing and imbedding might cause some alterations in the physical properties. From the great amount of data given in the foregoing tables it is possible to obtain some evidence bearing upon the question. The following table presents the general results obtained from the measurements of Zea.

TABLE XV.

MEASUREMENTS OF CELLS IN CURVED PORTIONS OF ROOTS OF ZEA.

	Convex	Concave	Convex	Concave
Normal roots, - - - - - -	(14.82	11.35	8.29	8.047)
Recurved to 15°, - - - - -	56.04	57.77	7.16	7.18
Geotropically curved 60°, - -	43.3	29.9	7.56	8.29
Mechanically curved 90°, - - -	61.4	56.85	6.98	8.04
Geotropically excited and mech. curved,	44.63	30.32	7.91	9.3
Geotropically curved 105°, - - -	48.05	24.7	6.98	11.4
Geotropically curved (old) 90°, -	71.99	45.00	8.53	11.69
Geotropically curved (old) 160°, - -	78.75	25.28	10.05	12.52

The comparison of the measurements of the cells of a region allowed to curve five hours, and then in the opposite direction for fifteen hours, with the curvatures of three and twenty hours duration is of interest. The length attained by the cells of the convex side in three hours is 43.3, and of the concave side is 29.9. The length of the cells of the concave side after recurvature of the portion apical to it is 57.7, and of the convex side 56.04. If it be taken for granted that the two measurements are of regions strictly correspondent, it can be assumed safely that during the five hours in which curvature was allowed to proceed normally the length of the cells of the convex side became greater than 43.3, and of the concave side greater than 29.9. On the reversal of the root and its excitation in the opposite direction, a curvature would be induced in a region a distance apical to the curvature of the shortest radius, by the amount of growth elongation of the tip of the root during five hours. The region of the new curvature would not be identical with that of the old, but would overlap a portion of it and extend apically a short distance. The new changes set up would affect the entire region of the old curvature by the mechanical strains set up. The compression of the concave side would be released, and the stretching of the convex side would be met. It would appear, therefore, that the cells of the convex side had undergone no contraction on the release of the first excitation, and had grown from 43 to 56 in fifteen hours. Then the cells of

the concave side on release from the compression have undergone an extension by which their length has been approximately doubled, and is in excess of the actual length of the cells of the convex side.

The conclusion is warranted that the excitation of the root in a direction opposite to newly formed curvature does not result in a straightening of the curvature by the relaxation or contraction of the extended convex cells, after a period of growth has ensued. The straightening of the curvature is due to the accelerated elongation of the concave side in the same manner as in the formation of the original curvature. A compression or shortening of the convex side does not occur until the concave side has extended sufficiently to compress it mechanically. It is pertinent to state here that anything like an active contraction or relaxation of the cells on the side becoming concave either in curvations or recurvations is not to be found in roots. On this account the straightening of curvatures by recurvation is not to be adduced as evidence that curvature is due to elastic stretching in the manner in which it has previously been done by Sachs, Noll, and others. Furthermore, my preparations show that the walls of the originally convex side have lost their attenuated condition, and that the cells of the originally concave side have taken up this character. The straightening of curvatures by plasmolysis is an altogether different process, since in this manner the greater elastic stretching of the convex side would be directly released, and would allow the root to return to a position determined by the physical characters of the wall. The complications which attend the plasmolysis of tendrils (14) would be wanting, and the straightening of the curvature in this manner, as well as the difference between the membranes of the convex and concave sides, would justify the conclusion that the curvature is due to the elastic stretching of the convex side of the root, and that this elastic extension was fixed or held in an elongated position by the loss of elasticity in any one of many ways; by changes of the quality of the wall induced by the ectoplasm, or by the intussusception or apposition of new building

material. The weight of evidence obtained by Noll and myself is in favor of the first named method.

The exact region of the motor zone which is set in activity by the impulse from the sensory zone embraces a part of the cortex consisting of the fourth to the eighth layer of the cortex in Zea, and from the fifth to the tenth or eleventh layer in Phoenix. The changes consequent upon a reception of an impulse occur in the walls of these cells only, and their active extension results in the stretching of the external or peripheral layers.

It must be supposed that the increase in elasticity extends to the radial walls in Phoenix. The folding of the walls of the motor cells of roots is doubtless due to the great resistance to their expansion offered by the peripheral layers. Marked or sharply folded walls are not to be found in the convex sides of stems and other organs in which all of the tissues are more or less active in the elongation.

The comparatively great radial growth of the epidermal cells of the concave side subsequent to curvature must be taken as a consequence of the mechanical strain exerted upon this layer.

XV. RECAPITULATION.

The contents of the foregoing paper may be summarized briefly in the following paragraphs:

1. In order to determine the nature and mechanism of a curvature, the phylogenetic meaning and purpose of the movement, the arrangement of the mechanical tissues, and the stage of development of the organ must be taken into consideration. The curvatures of stems are not identical with those of most tendrils, or of many roots.

2. It has been established beyond all doubt, by previous investigations, that curvatures are due to changes in the cell wall, rather than in the osmotic activity of the cell contents. The only determination of the real nature of curvature is to be accomplished by an anatomical examination of the cells of the motor zone before, during, and after curvature has taken place.

3. The development and organization of irritability in roots and shoots has been widely different. The segmentation and branching of the shoot, in order to facilitate food formation and reproduction, has been accompanied by an isolation and separation of the forms of irritability, a great extension of the sensory surfaces, and a less widely extended distribution of motor regions. The development of the root in order to facilitate absorption has resulted in a coincidence of many forms of irritability, both as to sensory and motor regions in the extreme apex of the growing organ which undergo branching but no segmentation.

4. The organs of the irritable mechanism of roots exhibit a physiological rather than a morphological differentiation.

5. The sensory zone. The mass of protoplasts of the root capable of converting certain external forces into forms of energy which induce movement constitutes the sensory zone. The term "perceptive zone" has hitherto been improperly applied to this region. Roots exhibit reaction to injuries which cut away a thin slice of the periblem, and to incisions in the periblem which do not affect the *punctum vegetationis*, as well as to incisions which cut away the *punctum vegetationis* entirely. Furthermore, injuries directly apical and affecting the *punctum vegetationis* alone do not cause reaction, and it is probable that the *punctum vegetationis* does not form an essential part of the sensory zone. The sensory zone, therefore, consists of a cup-shaped mass of periblem extending 1 to 2^{mm} axially, from which the bottom, represented by the *punctum vegetationis*, is lacking. The sensory zone extends approximately to the forward edge of the motor zone.

6. Transmission of impulses and latent period. The latent period of the reactions of roots varies from one to fifteen hours according to the nature of the stimulus and the mechanical qualities of the root. The latent period of geotropic reactions of Zea may be no more than one hour, of traumatropic reactions ten hours. The contiguity of the sensory and motor zones renders no special provision for the transmission of impulses necessary, and leads to the conclusion that the greater portion of the

latent period is consumed by the preliminary changes in the motor zone.

7. The motor zone. The movement of a root is caused by changes in the region in which the energy of the periblem is turned from cell division to cell enlargement. The motor zone includes a length of 2–3^{mm} of the root. The curvatures of roots apical and basal to the motor zone are mechanical accompaniments of the action of the motor zone.

8. The mechanism of curvature. The curvature of roots is due to the excessive active elongation of the internal layers of the cortex, of the side becoming convex, made feasible by the increased stretching capacity of the longitudinal membranes. The extension of the membranes is accompanied or preceded by changes in the quality of the membranes as indicated by their reaction to staining fluids. In consequence of the stretching the membranes of the convex side become thinner. As a later effect of the compression upon growth of the concave side, the membranes of that side become thicker. Seventy to one hundred hours later the difference is obliterated by growth.

The peripheral layers of the convex side are stretched passively in the longitudinal axis, and decrease in radial diameter during curvature. The peripheral tissues of the concave side are compressed longitudinally and show an increase in radial diameter during curvature. Roots with a peripheral layer of mechanical tissue exhibit only a slight increase of the radial diameter of the concave side and a marked increase of the radial diameter of the inner layers of cortex of the convex side. Roots without a peripheral layer of mechanical tissue exhibit a marked increase of the radial diameter of the inner cortex of the concave side, and a decrease of the radial diameter of the cortex of the convex side.

9. Recurvatures of stems in response to an excitation to movement in a direction opposite to the first curvature are not accompanied by a relaxation of the extended cells of the convex side of the first curvature, but by the greatly accelerated extension of the forward cells of the sensory and motor zones,

and render a second curvature in any region after an interval of three or more hours impossible. Recurvature in response to excitation is not therefore similar to straightening by plasmolysis.

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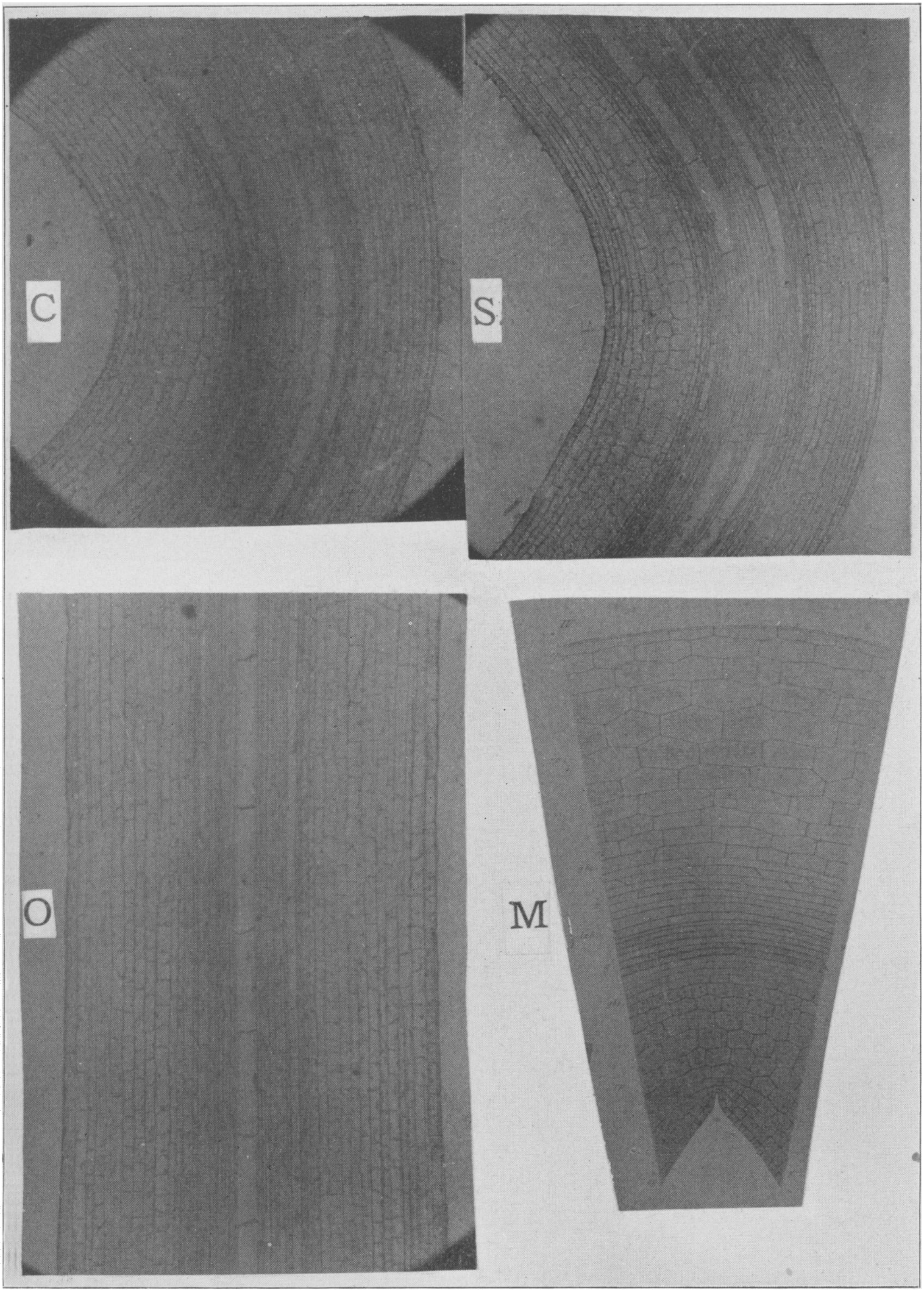
EXPLANATION OF PLATE XXVIII.

C. Median longitudinal section of motor zone of root of Zea geotropically excited and curved through 105°. The epidermal cells of the convex side have collapsed. A few root hairs are to be seen on the basal end of the motor zone. After a photomicrograph.

S. Median longitudinal section of motor zone of Zea geotropically excited and curved through 60°. The epidermal cells of both sides are normally turgid, and both exhibit root hairs. The differences between the contours of the cortical cells of the convex and concave sides are not so apparent as in C. After a photomicrograph.

O. Median longitudinal section of motor zone of straight root. After a photomicrograph.

M. Cieselski's drawing of a median longitudinal section of motor zone of Zea. "*Ep*, epidermis; *rp*, cortical parenchyma; *gbs*, endodermis; *lzb*, fibro-vascular bundle; *h*, wood cells; *g*, vessels. The cells of the half toward the nadir are smaller than those of the side toward the zenith; the cells of the upper half are stretched uniformly, while those of the under side are irregularly folded. The contents are much denser than of the upper side."



MACDOUGAL on ROOT CURVATURE.